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EFFECT OF SUBSTRATE ON SALMONID SPAWNING SUCCESS

by Dr. Dave Bennett

EFFECTS OF FINE SEDIMENTS ON THE SURVIVAL OF KOKANEE SALMON EMBRYOS IN THE NORTH FORK OF THE PAYETTE RIVER, IDAHO

BY D.H.Bennett & James W. Garrett

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Effects of Fine Sediments on the Survival of Kokanee Salmon Embryos in the North Fork of the Payette River, Idaho

Completion Report

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Executive Summary

1. Pre-emergent survival of kokanee embryos from redds formed in areas of groundwater upwelling was significantly higher than embryos spawned in areas lacking groundwater influence, although redds formed in areas of groundwater exhibited significantly lower surface water velocities and significantly greater fine sediment content.
2. As a result of higher incubation temperatures at upwelling sites, kokanee embryos were protected from freezing and exhibited increased rate of development as exhibited by longer and heavier alevins which may increase survival of fry recruiting to Payette Lake.
3. No significant relationships were found between hatching success and fines, water depth, and water velocity in sites lacking upwelling.
4. An increase in percent fines (< 0.83 mm) from September through March was not correlated to the Froude numbers or water velocity.
5. Spawning kokanee removed significant amounts of fine sediments during redd excavation from prespawn estimates and egg pockets contained more coarse gravels (19 - 76 mm) than tailspills.
6. Despite decreasing or stable flows, significant amounts of fines intruded kokanee redds, which suggests intrusion results from redistribution of fines from surrounding gravels rather than transport and deposition.
7. Higher spawner densities probably improve substrate quality over a larger area that may have survival benefits for incubating embryos.

8. This study found a significant positive relationship between female size (estimated by egg weight) and pre-emergent survival, although other factors (egg viability, density of egg deposition, surface-to-volume ratios) related to egg size favor higher survival of smaller embryos.
9. Increased survival of larger embryos spawned by larger females can be attributed to either a larger zone of cleaned gravels created by larger females or to more efficient fine sediment removal.

Introduction

Salmonid fishes of North America are an economically and aesthetically valuable resource. Perpetuation or enhancement of wild salmonids requires not only knowledge of life history traits and habitat requirements but also a thorough understanding of effects of habitat alteration. Interrelationships among salmonid fishes and their habitats are complex, and cumulative effects of seemingly insignificant habitat alterations can dramatically change the diversity and productivity of fish populations (Meehan 1991).

The ability of salmonids to migrate from lentic habitats into tributaries and successfully spawn is well documented (Northcote 1969a, 1969b; Raleigh and Chapman 1971; Stauffer 1972; Alexander and MacCrimmon 1974; Erman and Leidy 1975; Haynes and Nettles 1983; Neve and Moore 1983; Crisp et al. 1984; Bagliniere et al. 1989; Michael 1989). These studies focused on spawning migrations of adults and timing of emigration of juvenile fish. Salmonid spawning runs are generally initiated by change in water temperature, water quality, flow of spawning stream, or photoperiod (Reiser and Wesche 1977).

A knowledge of salmonid spawning behavior described as follows (from Reiser and Wesche 1977) increases the understanding of habitat requirements for successful reproduction. The spawning area is selected by the female who actively begins construction of the redd by turning on her side and rapidly flexing her caudal fin that loosens the substrate. Finer substrate is subsequently carried downstream by the water current. Continuation of this process results in a depression (pit) in the substrate and a mound (tailspill) just downstream formed by the deposition of the excavated material. When the redd is completed, the female, facing upstream, descends into the pit and is joined by the dominant male. The actual spawning lasts but a few seconds with eggs and milt deposited simultaneously. Afterward the female swims just upstream of the pit and again begins cutting and digging to cover the embryos and construct an additional pit in which to spawn if she is not spent. Multiple excavations by larger females may result in

the creation of several egg pockets.

The physicochemical characteristics of salmonid redd sites determine the condition and production of free-swimming young (Shumway et al. 1963). Adequate dissolved oxygen and removal of metabolic wastes are critical to the survival of buried embryos. A prolonged period of low dissolved oxygen resulting from low intragravel flows through the redd environment leads to low survival-to-emergence of salmonid embryos (Wickett 1954; Shumway et al 1963).

Historically, certain timber management activities and associated land-use practices have negatively impacted resident and anadromous fish populations (Gibbons and Salo 1973). Construction and maintenance of roads for timber management, recreation, and mining have been the main sources of fine sediment in adjacent streams (Bjornn et al. 1977). The sediment contribution per-unit-area from roads is often much greater than that from all other land management activities combined (Furniss et al. 1991).

Efforts to determine effects of fine sediments on salmonid reproductive success date to the early 1920s (Chapman 1988). Earlier studies were more observational than quantitative, but they established the basis for later research. Siltation was blamed for high mortality of steelhead Oncorhynchus mykiss (Shapovalov 1937) and coho salmon O. kisutch embryos (Shapovalov and Berrian 1939) placed in stream-fed, artificial troughs. Shaw and Maga (1943) reported poor incubation success of coho salmon embryos when mining silt was introduced into their troughs. Silt and sand were blamed for high mortality of chinook salmon O. tshawytscha embryos in a tributary to the Sacramento River, California (Gangmark and Broad 1955). Studies that followed focused on determining how fine sediments impair incubation success. Although the etiology of embryo mortality is poorly understood, research suggests that fine sediments fill interstitial spaces in the gravel and slow intragravel flows that reduce levels of oxygen to the developing embryos (Wickett 1954; Terhune 1958; Coble 1961; Cordone and Kelley 1961; Sheridan 1962; Shumway et al. 1963; Koski 1966; Mason 1969; Turnpenny and Williams 1980).

Subsequent research efforts have demonstrated an inverse relationship between quantity of fine sediment and incubation success (Koski 1966; Phillips et al. 1975; Hausle and Coble 1976; Tappel and Bjornn 1983; Reiser and White 1988). Research on rainbow trout (Witzel and MacCrimmon 1981; Sowden and Power 1985), brook trout Salvelinus fontinalis (Hausle and Coble 1976; Witzel and MacCrimmon 1983), brown trout Salmo trutta (Harshbarger and Porter 1982; Witzel and MacCrimmon 1983), Colorado River cutthroat trout O. clarki pleuriticus (Young et al. 1991), coho salmon (Phillips et al. 1975), chum salmon O. keta (Scrivener 1988) and chinook salmon (Tappel and Bjornn 1983; Reiser and White 1988) demonstrated reduced survival of embryos with increased amounts of fine sediments. Fine sediments (< 0.83 mm) constituting more than 10% to 20% of gravel composition significantly reduce survival-to-emergence of salmonids (Beschta and Jackson 1979; Turnpenny and Williams 1980; Tappel and Bjornn 1983; Chapman 1988; Reiser and White 1988) and result in decreased size of emerging alevins with a corresponding decrease in survivability (Shumway et al. 1963; Koski 1966; Phillips et al. 1975; Tappel and Bjornn 1983).

Although extensive research has quantified the adverse effect of fine sediment on survival-to-emergence and fitness of emerging alevins, most studies have involved laboratory simulations using artificial stream channels or troughs, which may or may not accurately reflect reproductive success of stream-spawning salmonids. Chapman (1988) argued that results from laboratory studies, in spite of the elegance of approach and resultant data, are applicable to conditions in the laboratory. He (1988) further stated that laboratory studies of embryo survival in relation to percentages of fine sediments should be regarded as models useful in assessing mechanistic responses, rather than as analogs of nature that permit accurate assessment of quantitative biological responses in actual redds. Findings from laboratory experiments need confirmation in field studies before results can be viewed as representative of responses exhibited under variable natural conditions in streams.

Research is also needed to describe transport of fine sediment and to quantify rates of intrusion into salmonid redds. Laboratory studies frequently use predetermined gravel composition or one-time application of fine sediments; these studies do not reflect the changing nature of gravel composition under variable natural conditions. Timing of fine sediment deposition into salmonid redds may prove a critical variable in studies of survival-to-emergence. Other factors affecting pre-emergent survival, such as use of groundwater upwelling for spawning and the effects of female size and subsequent redd size, have received limited investigation (Ottaway et al. 1981; Sowden and Power 1985; Crisp and Carling 1989). The purpose of this study was to determine factors affecting pre-emergent survival of kokanee O. nerka embryos in the North Fork of the Payette River (NFPR), Idaho. These studies assessed effects of physical habitat variables including upwelling on the spawning success of kokanee, measured the rates of fine sediment intrusion into natural kokanee redds, and evaluated the evidence of increased survival of larger kokanee embryos in a heavily sedimented stream.

Objectives

1. To relate physical habitat variables, including upwelling sites, to incubation success of kokanee embryos in the NFPR;
2. To evaluate substrate alteration by spawning kokanee and subsequent intrusion of fine sediments during incubation in the NFPR; and
3. To evaluate the evidence of increased survival of larger kokanee embryos in a heavily sedimented stream.

Study Area

The NFPR is located in northwest Valley County, Idaho (Figure 1). The NFPR drainage is part of the central Idaho batholith, a 41,400 km^2 expanse of intrusive, acid, igneous rock (Bjornn et al. 1977) that is characterized by steep slopes, heavily dissected topography, and highly erodible soils (Platts et al. 1989). Elevations in the basin north of McCall, Idaho, range from 1533 m at Payette Lake to greater than 2800 m. Annual precipitation, primarily snowfall, ranges from 76 to 150 cm.

Historically, Payette Lake supported sockeye salmon O. nerka. In the late 1880s, 75,000 kokanee and sockeye were harvested annually in the NFPR (Everman 1896). Sockeye runs were blocked by hydroelectric dams on the Payette and Snake rivers in the 1930s. Kokanee remain and comprise the primary sport fishery in Payette Lake (Grunder and Anderson 1991), and adult kokanee, estimated at 59,300 in 1993, spawn in the lower 7 km of the river (Bennett and Frost 1995). This reach of the NFPR averages 22 m in width (range 4.5 - 58.6 m) and is characterized as a moderately braided, meandering stream. Flows in the NFPR are partially controlled by three low-head dams at Upper Payette Lake on the NFPR, Box Lake on Box Creek, and Granite Lake on Fisher Creek. Flows average from 0.92 to 1.4 m^3/s in September, decrease to base flow (0.34-0.4 m^3/s) in August, and remain low until commencement of runoff in late-March. Spawning begins in late August and peaks in mid- to late September (Bennett and Frost 1995). Timber harvest in the upper reaches of the drainage has had deleterious effects on fish habitat due to loading of fine sediments, especially downstream of Fisher Creek, the reach most used by spawning kokanee (USDA 1991).

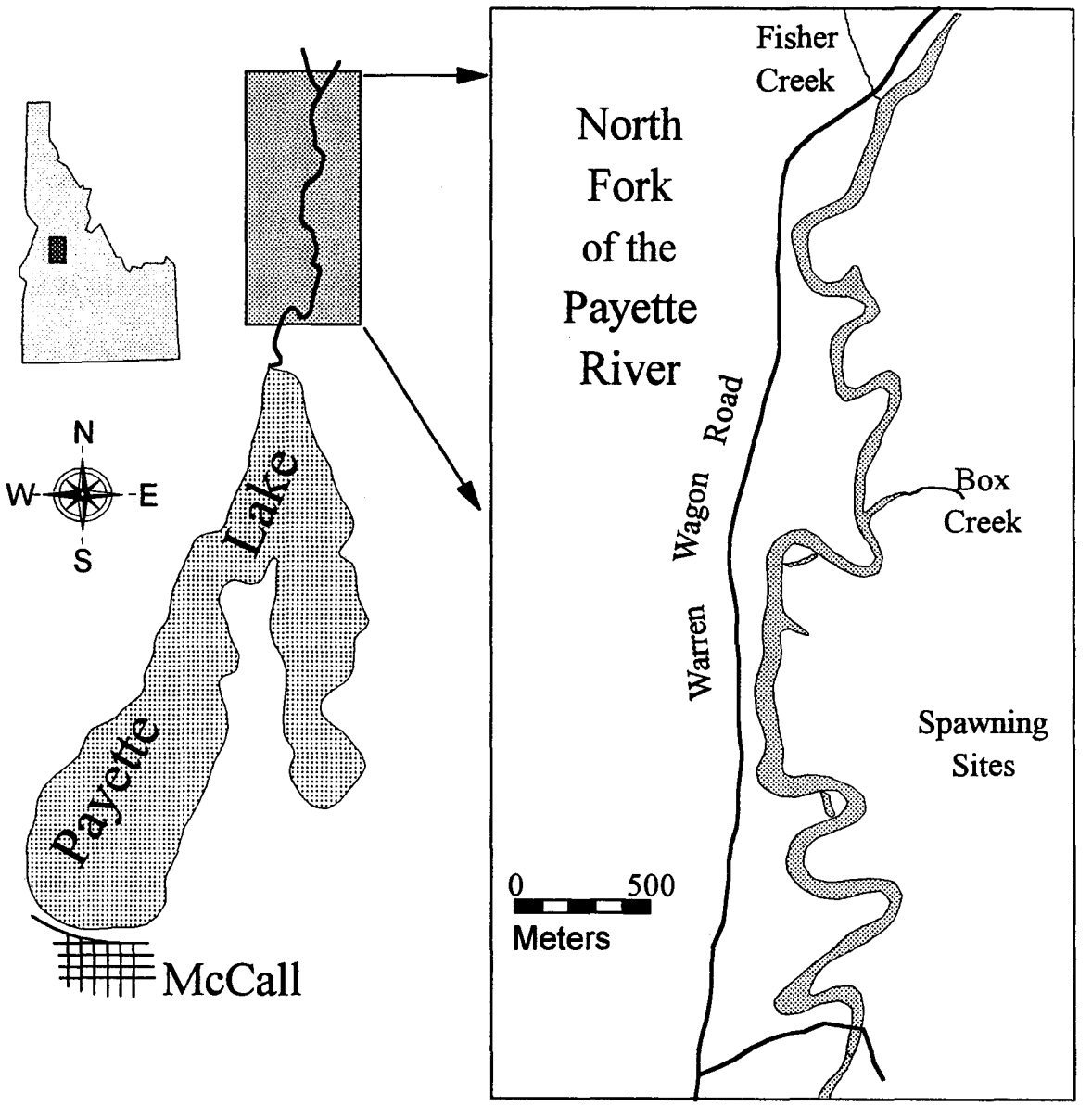

Figure 1. Location of the North Fork of the Payette River, Idaho, and the reach (on right) that was sampled in 1993 to 1994.

Objective 1: To relate physical habitat variables, including upwelling sites, to incubation success of kokanee embryos in the North Fork of the Payette River.

Abstract

Kokanee Oncorhynchus nerka spawned in areas of groundwater upwelling in the North Fork of the Payette River, Idaho. Intragravel water temperatures in redds exceeded surface water temperature by 2.4 to 2.6°C. Although redds constructed in upwelling sites contained significantly more fine sediments (< 0.83 mm) and were constructed in areas of significantly lower surface water velocities than redds not influenced by upwelling, pre-emergent survival of fry from redds in upwelling sites (84%) was significantly higher than that from redds in other areas (66%). Higher incubation temperatures at upwelling sites accelerated rates of development of embryos, protected embryos from freezing, and may have increased survival of kokanee fry recruiting to Payette Lake.

Introduction

The sockeye salmon Oncorhynchus nerka is the only species of Pacific salmon that has formed natural freshwater populations (Gipson and Hubert 1993). Kokanee O. nerka, the landlocked form in North America, is present in much of the range of the sockeye O. nerka from the Klamath River, California, north to Point Hope, Alaska, (Scott and Crossman 1973) and has been successfully introduced to many coldwater systems as a sport and forage fish (Wydowski and Bennett 1981).

Kokanee, the primary sport fish of Payette Lake, has been in decline during the past 20 years and recent data indicate recruitment from the North Fork of the Payette River (NFPR) is insufficient to optimally seed the lake (Grunder et al. 1991). Since land-use activities in the upper reaches of the drainage have caused significant loading of fine sediments (USDA 1991), mortality of incubating kokanee embryos due to increased fine sediment may be the primary factor limiting production of fry. Managers need a better

understanding of the relationship between physical habitat attributes and incubation success to develop viable fishery enhancement programs.

Upwelling sites are especially attractive to spawning salmonids. Current knowledge on effects of groundwater or spring upwelling on salmonid incubation success is limited (Hansen 1975; Carline 1980; Sowden and Power 1985). Bjornn and Reiser (1991) reported that upwelling may enhance embryo survival by providing a more stable thermal environment and increasing the water exchange rate past embryos if sufficient oxygen levels exist. Sheridan (1962) documented warmer winter water temperatures at upwelling sites, but he concluded that most intragravel dissolved oxygen downwelled from the stream. While most studies have demonstrated inverse relationships between fine sediment composition and embryo survival (Phillips et al. 1975; Hausle and Coble 1976; Tappel and Bjornn 1983) and between fine sediment composition and size of emerging fry (Shumway et al. 1963; Koski 1966; Phillips et al. 1975; Tappel and Bjornn 1983), incubation success and fry quality may be independent of substrate quality in areas of groundwater upwelling with sufficient (> 6.0 mg/L) dissolved oxygen (Sowden and Power 1985; Bjornn and Reiser 1991).

Use of spring or groundwater upwelling sites for spawning has been reported for sockeye (Lister et al. 1980; Lorenz and Eiler 1989), pink salmon O. gorbuscha (Krueger 1981), rainbow trout O. mykiss (Sowden and Power 1985), and brook trout Salvelinus fontinals (Hansen 1975; Snucins et al. 1992; Curry et al. 1994). No known studies have reported use of upwelling areas by spawning kokanee, and none have compared incubation success of salmonids spawning in upwelling sites to cohorts spawning in areas unaffected by upwelling..

In this study, we related pre-emergent survival of kokanee embryos in the NFPR to various physical habitat variables. Additionally, we assessed the use of groundwater upwelling areas by spawning kokanee and compared pre-emergent survival, water depth, and water velocity, and fine sediment composition of kokanee redds in upwelling areas to

redd sites lacking evidence of groundwater inflow.

Methods

Kokanee redds were located in the NFPR and marked during peak spawning from 19 through 29 September 1993. In all, 100 kokanee redds were identified and marked in 11 distinct spawning sites (Figure 2). Each site was enclosed with 3.8-cm mesh fencing to prevent further spawning. The fencing was removed when most spawning activity ceased in mid-October 1993. Each fenced site encompassed 6 to 14 kokanee redds, and individual redds were identified by their characteristic pit and tailspill and marked by driving a numbered reinforcing bar into the substrate at the center of the pit. Egg pockets of salmonids are typically found under the leading edge of the tailspill (Chapman 1988). Water velocity (Swoffer Instruments, Seattle, Washington) was measured at the estimated egg pocket location on the upstream face of the tailspill. Two to four redds adjacent to fenced sites (2 to 4 redds per site) were marked and numbered similar to redds in the enclosures. These redds had similar water depth, water velocity, and visual substrate quality to redds in the enclosures. Conditions were highly uniform throughout these spawning areas.

Spring sampling began on 11 March 1994 when most spawning areas were free of snow and ice. Two to four redds adjacent to spawning sites and one to three randomly selected redds within each site were identified by the numbered reinforcing bar and were sampled for substrate with a 15.5-cm hollow core sampler (McNeil 1962) approximately 15 to 20 cm deep at the estimated egg pocket location (Table 1). Surrounding gravels filled the slight depression that remained when the sampler was removed. Substrate samples were transported to the University of Idaho laboratory where they were dried for 4 days at 101°C and mechanically sieved for 1 minute through 12 U.S. Geological Survey standard sieves with mesh sizes ranging from 0.25 to 76 mm. To eliminate sampling bias, particles larger than 25 mm were excluded from the analysis (Adams and Beschta 1980; Chapman

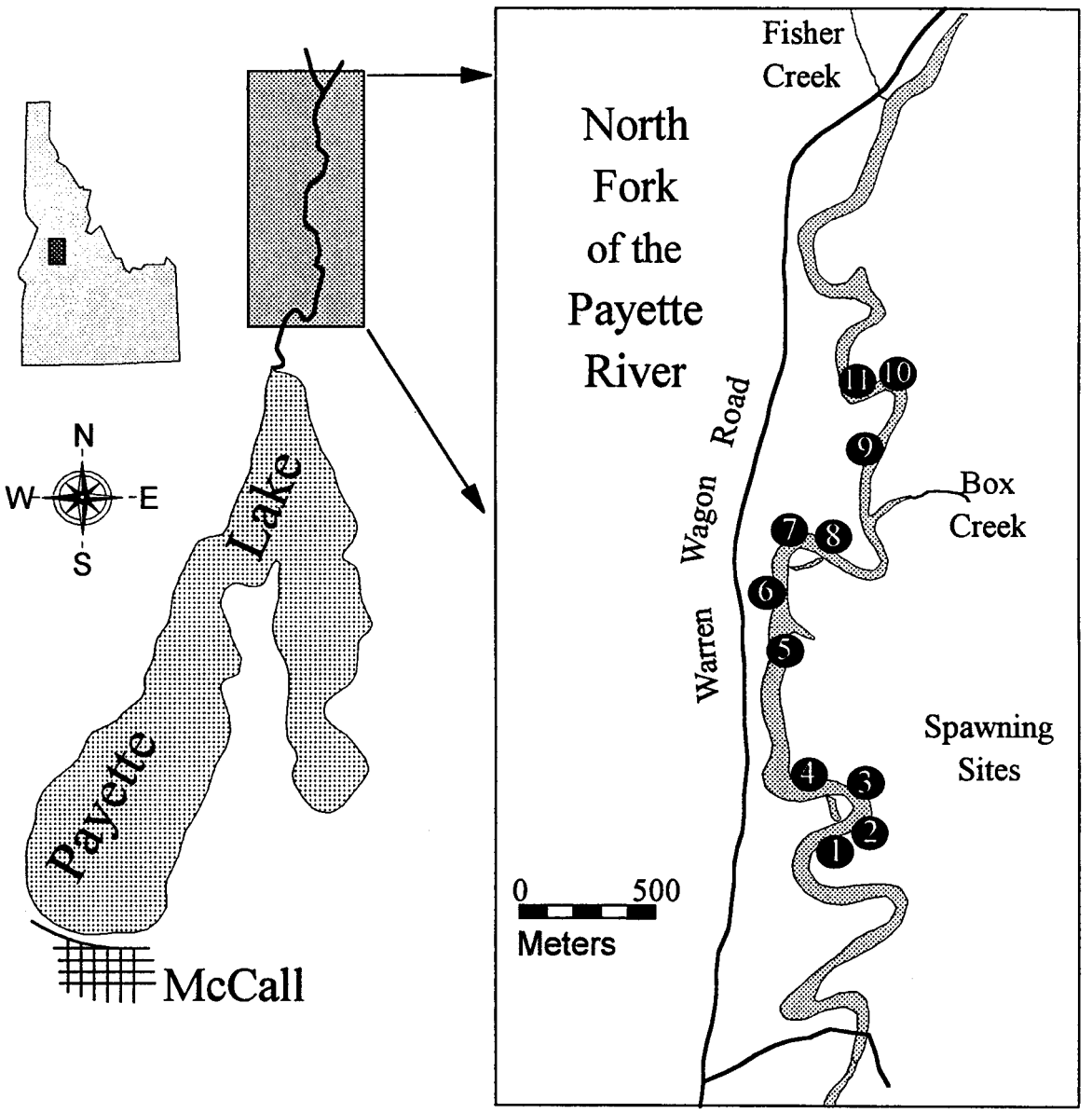

Figure 2. North Fork of the Payette River, Idaho, kokanee spawning sites sampled in 1993 to 1994.

Table 1. Number of kokanee redds marked per spawning site and the number of redds core sampled inside and outside enclosures. Redds outside enclosures were core sampled only. Redds inside enclosures were hydraulic sampled and randomly selected redds were core sampled for substrate composition.

Site number	Number of redds marked	Number of redds cored	
		Inside	Outside
1	14	2	3
2	14	3	3
3	10	2	4
4	10	2	4
5	8	1	4
6	8	0	3
7	7	2	3
8	8	2	4
9	6	2	2
10	7	2	2
11	8	0	2

et al. 1986; Young et al. 1991). Sieve sizes were then converted to categories of substrate size and percent fine sediment (< 0.83 mm) was calculated. Mean percent fines (< 0.83 mm) were calculated for each site and used as an estimate of gravel quality for those redds lacking substrate samples at each site.

Redds located in the enclosures, not previously sampled by the core sampler, were sampled hydraulically (McNeil 1964; Magee and Heiser 1971). A portable water pump rated for 2.2 L/s was used to pump water from the river. A 0.8-m metal wand was mounted at the end of a 15.2-m long, 2.5 cm diameter house. An air-water mixture was created by water that pumped through the hose and air that seeped through a vent on the wand. During sampling, the wand was inserted into the redds and rigorously moved for 2 minutes through an area approximately 0.5 m^2 believed to contain the egg pocket. The air-water mixture lifted dead and live eggs and alevins up and into the water column where they were collected in a 2.2-m^2 drift screen constructed of 2-mm nylon netting. Live and dead embryos and alevins were preserved in 10% formalin until they were measured. Lengths of embryos and alevins were measured using an optical micrometer and weights were measured after embryos and alevins were blotted dry.

Water temperatures at the water-substrate interface and below the substrate surface were obtained at each site on 14 March 1994 with a YSI Model 57 meter (Yellow Springs Instruments, Yellow Springs, Ohio). Intragravel temperature measurements were obtained by burying the probe 10 cm beneath the gravel and waiting 10 minutes prior to reading. We used differences greater than 1.5°C between intragravel temperatures and surface water temperatures as evidence of groundwater upwelling (Lorenz and Eiler 1989).

A concurrent study found minimal (< 3%) loss of dead eggs during incubation and, therefore, the number of dead eggs or embryos was not adjusted for losses due to decomposition or invertebrate predation (Garrett and Bennett, unpublished data). Arcsine transformation of percent hatching success was not required as most proportions ranged from 30% to 70% (Steele and Torrie 1980). Samples collected from redds containing less

than 25 eggs or alevins (dead or live) were excluded from analysis. Regression analysis was used to relate incubation success to physical habitat variables of depth, velocity, and substrate. Hierarchical (nested design) analysis of variance (Zar 1984) was used to compare incubation success, water depth, water velocity, and fine sediment (< 0.83 mm) composition between redds influenced by groundwater upwelling to those unaffected by upwelling. We compared a random sample of lengths and weights of alevins from upwelling versus nonupwelling sites using a t-test. Significance was determined at $P < 0.05$.

Results

In all, 87 of the 100 marked redds were hydraulically sampled. Thirteen redds could not be sampled due to excessive snow and ice in the area. Forty redds were eliminated from analysis due to complete or partial dewatering and freezing, leaving 47 redds available for analysis.

Intragravel water temperatures on 14 March 1994 for sites #8 and #10 were 2.6°C and 2.8°C, respectively. Water temperature at the water-substrate interface was 0.2°C at both sites, indicating the presence of groundwater upwelling. Alevins collected from these two sites exhibited advanced development and most were fully buttoned (24.5 mm). Alevins sampled from sites with groundwater upwelling were significantly ($P < 0.0001$) longer (24.5 mm) than alevins (18.9 mm) from sites lacking upwelling. Mean weight of alevins sampled from areas with upwelling was significantly ($P = 0.00104$) higher (66.5 mg) than that (61.7 mg) of alevins from sites lacking upwelling. Live samples collected from the remaining sites (34 redds), where intragravel water temperatures were similar to surface water temperatures, consisted of viable embryos and/or recently hatched alevins markedly less developed than those from sites #8 and #10.

For sites lacking groundwater upwelling, multiple regression failed to reveal significant relationships between hatching success and fines ($P = 0.47$), water depth

(P = 0.24), or water velocity (P = 0.13). Although fine sediment content was significantly (P = 0.002) correlated to hatching success, the relationship was weak (r^2 = 0.01). Hatching success for 13 redds in sites with groundwater upwelling (mean 84.3%; 95% C.I.78.8 - 89.7%) was significantly (P = 0.02) higher than for 34 redds lacking upwelling (mean 65.6%; 95% C.I. 56.6 - 74.6%; Figure 3). Mean percent fine sediment (< 0.83 mm) for redds in upwelling areas (17.4%; 95% C.I. 15.4 - 19.4%) was significantly (P < 0.001) higher than that for redds in other areas (9.4%; 95% C.I. 8.4 - 10.1%). Fine sediment content differed significantly (P = 0.001) within upwelling and nonupwelling sites due to mean percent fines in site #10 (20.4%) being significantly (P < 0.001) higher than in site #8 (13.8%). Water velocity measured at redds in upwelling sites (11.5 cm/s; 95% C.I. 6.6 - 16.4 cm/s) was significantly (P < 0.001) lower than at redds in nonupwelling areas (38.2 cm/s; 95% C.I. 32.8 - 43.7 cm/s). Mean water depth of redds in upwelling areas (22.7 cm; 95% C.I. 19.0 - 26.4 cm) was not significantly (P = 0.86) different than that of redds in other areas (22.4 cm; 95% C.I. 20.4 - 24.4 cm). Forty redds could not be further analyzed, however, because of high mortality presumably caused by dewatering or freezing.

Discussion

Kokanee in the NFPR were observed spawning at high densities in a few discrete areas upstream from Payette Lake. Two of the 11 spawning sites in this study exhibited evidence of spring or groundwater upwelling. In this study, redds formed in sites with groundwater upwelling exhibited higher pre-emergent hatching success, although formed in areas of lower water velocities containing higher fine sediment content than redds formed in sites without groundwater upwelling. Low water velocities and high fine sediment content were also reported in areas of upwelling known for sockeye spawning (Lorenz and Eiler 1989).

No strong relationships were revealed between hatching success exhibited in redds

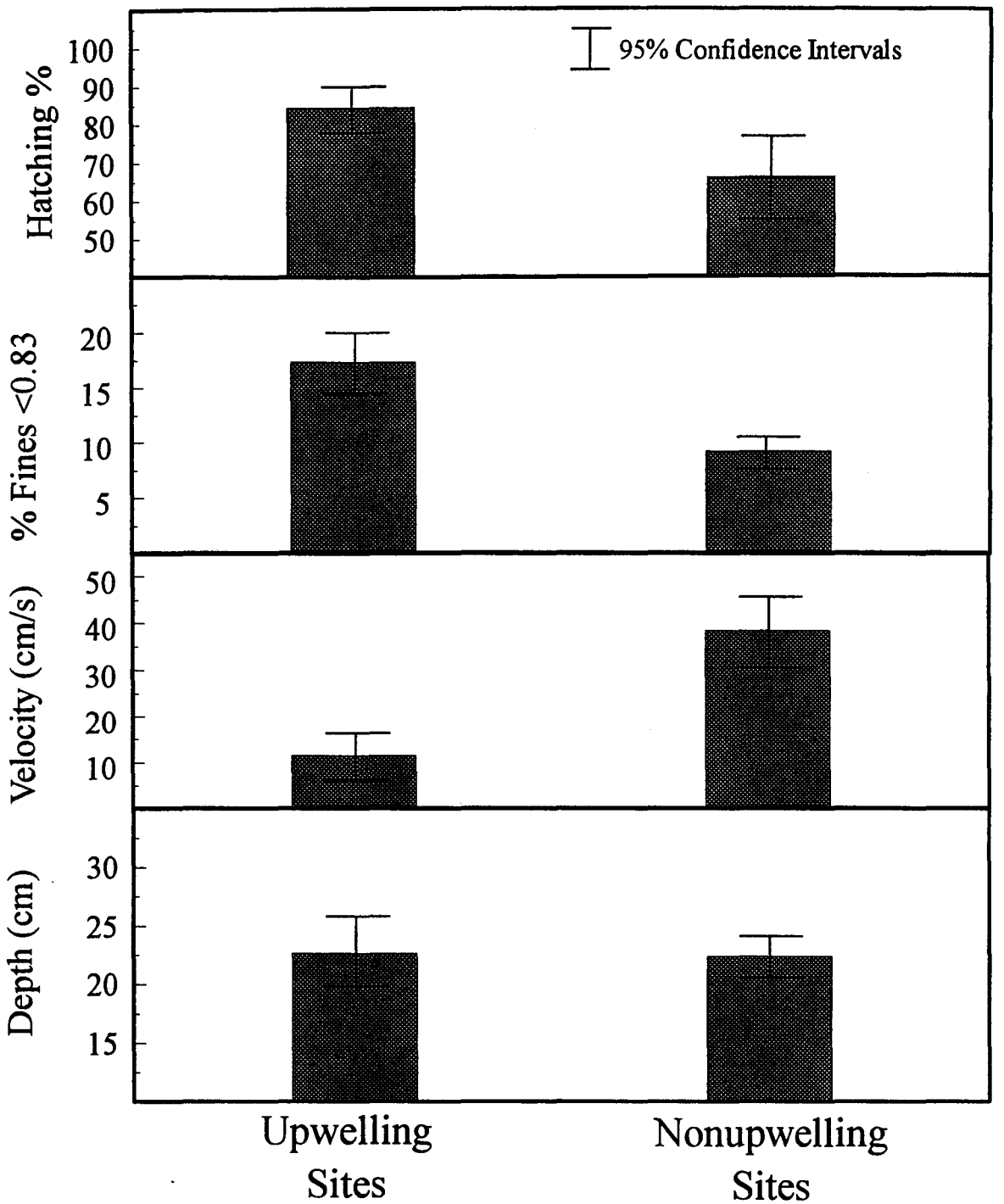

Figure 3. Means and 95% confidence intervals for hatching success, percent fine sediment (< 0.83 mm), water depth, and water velocity of redds constructed in areas of groundwater upwelling and areas lacking evidence of groundwater upwelling.

lacking influence of groundwater upwelling and physical habitat variables. This is likely due to the narrow range of fine sediment content in these redds. While hatching success exhibited in these redds ranged from 1% to 96%, the percent fines smaller than 0.83 mm ranged from 4.96 to 14.2, and 27 of 34 redds had fine sediment content that measured from 6% to 11%. The narrow range of variability in these redds suggests that other factors, such as egg depth and embryo size (Objective 3), had a greater influence on survival than percent fine sediment.

Forty redds were excluded from this analysis due to high mortality attributed to dewatering or freezing. Flows in the NFPR decline through fall, and we observed numerous marked redds that were exposed and frozen in November. We can only speculate on the effects of redd dewatering and freezing, as the effects of freezing of incubating embryos were not assessed because redds could not be observed during mid-winter. Dewatering may not necessarily result in high mortality unless embryos are frozen or desiccate. Reiser and White (1981) reported 24% mortality of chinook salmon O. tshawytscha embryos as a result of desiccation. Some redds used in analysis may have been dewatered for brief periods and protected from freezing by snow cover. Some sites exhibited dewatering that was evident during March sampling, however, differential effects of dewatering could not be determined. For example, enclosure #3 contained seven redds that exhibited total mortality and one redd that had high (87%) survival, which was the only redd at this site with water depth greater than 15 cm. Although some redds may be dewatered with minimal results, we speculate that dewatered redds will generally exhibit high mortality, possibly from freezing. Since 40% of our marked redds exhibited high or total mortality, which we attribute to dewatering and freezing, limiting water withdrawal and flow reductions during fall and winter would increase fry survival.

Redds located in upwelling sites and in poor or marginal habitats were initially enclosed and marked. Seven redds at these two sites sampled in March had water velocities lower than 10 cm/s, of which four were constructed in sites without any

measurable velocity. The higher survival in upwelling sites containing higher proportions of fine sediment supports the contention that embryo survival can not be predicted based solely on substrate characteristics in groundwater-fed streams (Sowden and Power 1985; Bjornn and Reiser 1991). Flow in the NFPR is less variable than in unregulated streams. Sheridan (1962) indicated that most groundwater originates from rain or snow-melt, and dissolved oxygen levels, dependent on biochemical oxygen demand as it percolates through ground, may vary considerably. Although we did not measure dissolved oxygen levels at these sites, adequate oxygen must have been present because of the high survival rates observed in these areas.

Whether kokanee can determine areas of groundwater upwelling sites by temperature differential is unknown. Perhaps they return to these sites due to strong homing traits. If these sites were highly attractive to kokanee, however, numerous kokanee would spawn there. They did not, which suggests homing may be an important factor governing their use of these areas. Freshly excavated redds in upwelling sites lacked the characteristic pit-and-tailspill morphology. Instead, redds in these areas consisted of larger cobble that had been swept clean of overlying sand and fine particles. The resulting redd exhibited a "nest-like" appearance similar to that described by Snucins et al. (1992) for brook trout spawning in upwelling areas. Deposited eggs likely fell into crevasses and were deposited at depths more shallow than normally associated with salmonid redd formation. During hydraulic sampling of these redds, dead embryos and alevins were excavated from depths obviously more shallow than those at other sites.

Lorenz and Eiler (1989) identified three advantages to spawning in upwelling areas. First, the hydraulic action of upwelling groundwater provides a loose and unconsolidated substrate for spawning and fry emergence. Second, fry may have developed a specialized behavior to emerge from gravel beds covered by uncompacted fine sediments (Bams 1969). Third, upwelling groundwater provides a more constant incubation temperature and may not freeze as readily as surface water, as freezing can be common in harsh winter

conditions (Reiser and Wesche 1979) and in the NFPR.

Alevins from sites with groundwater upwelling were significantly longer and heavier than those from sites lacking groundwater upwelling. Because of the higher water temperatures in upwelling sites, however, the larger size of alevins may be attributed to a more advanced stage of development. We believe that alevins gain weight as high density, low-water-content yolk is metabolized into tissue that is approximately 70% to 80% water. Alevins from upwelling sites were more advanced and had fully absorbed their yolk sac prior to the spring freshet as compared to most of the alevins from sites lacking upwelling.

One limitation of our sampling was that we assessed embryo survival prior to emergence. Early sampling may have inflated our estimates of survival as higher mortality may occur during emergence. Increased rate of embryo development associated with warmer incubation temperatures may provide the most important advantage to kokanee spawning in areas of groundwater upwelling. The advanced stage of development likely results in higher survival in Payette Lake. Increased embryo survival associated with larger size (Shumway et al. 1963) may increase the capabilities of fry to avoid predators while recruiting to Payette Lake. Larger size of fry at recruitment should result in higher first year growth. The variability of kokanee spawning site selection also decreases the likelihood of a major year-class loss should a catastrophic early-season flood event scour redds containing embryos or less-developed alevins. Although comprising a small portion of the spawning stock, adults spawning in upwelling sites may be important to the long-term viability of the self-sustaining kokanee population in the NFPR.

Objective 2: To evaluate substrate alteration by spawning kokanee and subsequent intrusion of fine sediments during incubation in the NFPR.

Abstract

We measured substrate alteration by spawning kokanee Oncorhynchus nerka in the North Fork of the Payette River, Idaho. Mean percent fine sediment (< 0.83 mm) of egg pockets (9.1%) and tailspills (13.4%) were significantly lower than that for the prespawning condition (17.1%). Samples from egg pockets contained significantly more coarse gravels (19 - 76 mm) than those of tailspills. Although flows were decreasing during spawning and stable during incubation, we measured significant increases in fine sediment composition of egg pockets. Our findings indicate that fine sediments intrude into kokanee redds as small particles redistribute from adjacent gravels. Therefore, high density of spawning kokanee may improve the quality of substrate for spawning and have survival benefits for incubating embryos.

Introduction

Fine sediments reduce survival of embryos to emergence (Tappel and Bjornn 1983; Irving and Bjornn 1984) and size of embryos at emergence (Shumway et al. 1963; Koski 1966; Phillips et al. 1975; Tappel and Bjornn 1983) of various salmonid fishes. Fine sediments fill interstitial spaces and reduce intragravel velocities, thereby reducing delivery of oxygen to and nitrogenous wastes from incubating embryos and alevins (Wickett 1954; Coble 1961; McNeil and Ahnell 1964; McNeil 1966). Fine sediments also can entomb alevins, precluding lateral or vertical movement and emergence (Phillips et al. 1975; Hausle and Coble 1976; Witzel and MacCrimmon 1981). Particles smaller than 0.83 mm may reduce embryo survival more than other size classes of substrate (Reiser and White 1981; Tappel and Bjornn 1983).

Young et al. (1989) reviewed several studies that quantified fine sediment removal

by spawning anadromous salmonids. Chapman (1988) described redd construction and indicated that female salmonids remove fines from an area much larger than the actual egg pocket, although they deposit eggs adjacent to particles that may be too large for the female to move. Grost et al. (1991) reported that nonanadromous salmonids remove fines during redd construction, however, most studies on substrate modification have focused on larger anadromous salmonids (Everest et al. 1987) than smaller resident fishes (Young et al. 1989).

Small particles gradually intrude into the relatively clean gravels of the completed redd (Chapman 1988). Most research that relates fine sediment composition to salmonid incubation success has involved laboratory studies in artificial stream channels or troughs in which embryos placed within a container are buried in stream gravels (Tappel and Bjornn 1983; Reiser and White 1988). Because of difficulties in quantifying relationships between substrate composition and embryo survival, most studies resort to controlled laboratory experiments (Witzel and MacCrimmon 1983). Although Stowell et al. (1983) suggested that predictions of embryo survival may be based on substrate samples collected before spawning, embryo survival depends not upon the condition of spawning gravel before or immediately after spawning but conditions during the weeks and months of incubation (Lisle and Lewis 1992). Any changes in redd gravel quality that occur are likely to vary widely between streams and years depending on topology, geology, land-use practices, precipitation patterns, and flow regimes. Koski (1975), Meehan and Swanston (1977), and Beschta and Jackson (1979) investigated intrusion of fines into redds in laboratory experiments. Grost et al. (1991) estimated intrusion of fines into brown trout Salmo trutta redds in a Wyoming stream. Their study, however, compared substrate composition of redds in winter (late incubation) to that of freshly formed redds the following fall, which could not account for differences in years (precipitation and flows) or redd site selection. Thurow and King (1991) measured temporal changes in sediment during incubation by sampling natural steelhead O. mykiss redds at varied intervals during

embryo incubation. They did not detect any significant temporal changes in redd pits or tailspills and were unable to sample sufficient egg pockets to measure changes. Our objectives were (1) to evaluate alteration of substrate used by kokanee Oncorhynchus nerka during redd excavation and compare results to those reported by Young et al. (1989) for brook trout Salvelinus fontinalis, and (2) to measure changes in fine sediment composition during the incubation period and relate intrusion to hydraulic variables.

Study Area

Kokanee redds were sampled downstream from Fisher Creek in the North Fork of the Payette River (NFPR) in northwest Valley County, Idaho (Figure 1). Kokanee O. nerka, estimated at 59,300 in 1993, spawn in the lower 7 km of the NFPR (Bennett and Frost 1995). This meandering, moderately braided reach of the NFPR averages 22 m in width (range 4.5 - 58.6 m). Flows in the NFPR are partially controlled by three low-head dams at Upper Payette Lake on the NFPR, Box Lake on Box Creek, and Granite Lake on Fisher Creek. These reservoirs are used to augment flows for late summer irrigation further downstream. Evacuation of these reservoirs resulted in peak flows of 3.8 m^3/s on 7 September 1993 (Bennett and Frost 1995), whereas flows gradually decrease to base flow (0.34 - 0.40 m^3/s) by October and remain low and stable until commencement of runoff in late-March. Spawning commences in late August with peak spawning occurring in mid- to late September during decreasing flows (Bennett and Frost 1995).

Methods

We located and marked kokanee redds during peak spawning from 19 through 29 September 1993. For this study, we identified 44 kokanee redds; 28 in three distinct spawning sites (A - C; Figure 4) and 16 adjacent to 11 spawning sites (#1 - 11; Figure 2). To the extent possible, we chose redds that were at least 2 to 3 m apart and not directly upstream or downstream from other redds. We believed this would eliminate or minimize

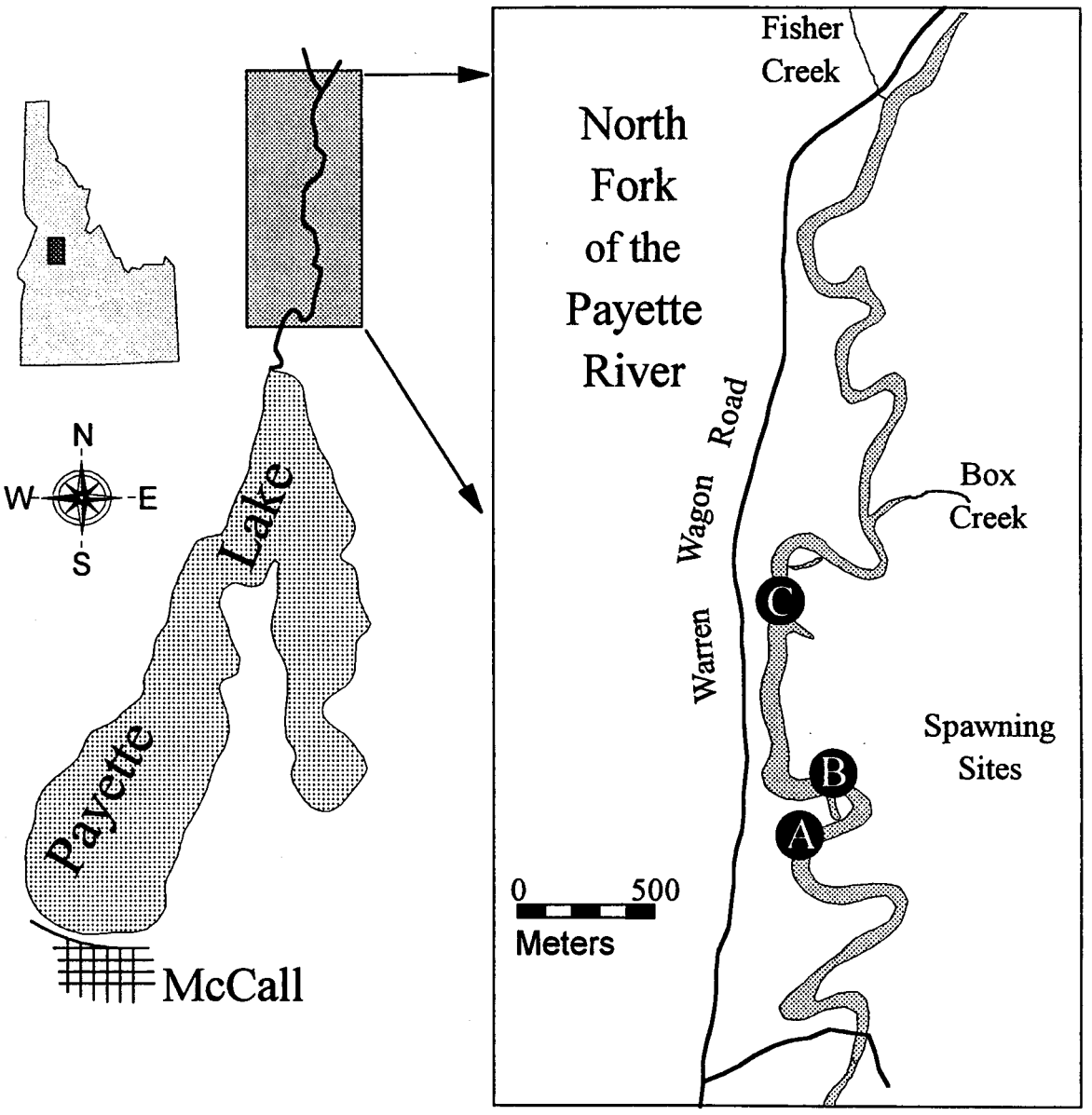

Figure 4. Three sites (A-C) in the North Fork of the Payette River, Idaho, containing kokanee redds sampled in 1993 to 1994.

the risk of fine sediments stirred from our sampling being deposited on other marked redds. For the same reason, we sampled in an upstream direction during spring. Methods for identifying, marking, fencing, and sampling were similar to those described in Objective 1.

We obtained substrate samples on 44 redds at their estimated egg pocket location and at tailspill crest using a 15.5-cm hollow core sampler (McNeil 1962) from 21 through 26 September 1993. The core sampler removed a small amount of gravel, and surrounding gravel filled the slight depression that remained when the sampler was removed. Presence of kokanee embryos and distance from the reinforcing bar (at pit center) to estimated egg pocket location was recorded to ensure subsequent sampling at the same location. Samples of undisturbed substrate that we believed representative of conditions before spawning were obtained adjacent to spawning sites (2 to 4 per site). Mean percent fine sediment (< 0.83 mm) content of these samples was used as estimates of gravel quality before spawning. We subsequently sampled egg pocket locations on 18 randomly selected redds from 10 through 12 November 1993 and on 25 redds from 11 through 14 March 1994 prior to emergence. Substrate samples were analyzed similar methods used in Objective 1.

Chapman (1988) stated that Froude (F_r) numbers, freshets, and sediments in transport strongly influence conditions in the redd during incubation and emergence. He stated that F_r help characterize flow conditions that influence intrusion of fines. Froude numbers are calculated as (Streeter and Wylie 1975):

$$F_r = V^2/gy;$$

where: V = mean velocity (m/s);

g = acceleration due to gravity (9.8 m/s^2); and

y = depth of flow (m).

We calculated this dimensionless variable from September water depth and water velocity measurements for each redd to determine if the amount of fine sediments intruding into

redds was associated with or influenced by F_r.

We found with a Shapiro-Wilk's W-test that data on percent fine sediment (< 0.83 mm) were not normally distributed (P < 0.02), while coarse gravel (19 - 76 mm) compositions were normally distributed (skewness < 0.35; W = 0.98; P = 0.96). To determine significant differences between prespawning and postspawning (egg pocket and tailspill) fine sediment content, we used the Mann-Whitney U-test (Daniel 1990). We compared coarse gravel content between September egg pocket and tailspill samples with a paired t-test. We compared fine sediment (< 0.83 mm) composition with a Wilcoxon matched-pairs signed-ranks test and compared fine sediment content in egg pockets between the two sample dates (September, November, March) using Friedman's two-way analysis of variance by ranks, a nonparametric analogue of the parametric two-way analysis of variance (Daniel 1990). We used Spearman's rank correlation to determine relationships between prespawning conditions, postspawning egg pocket substrate, and tailspill substrate. Because hydraulic parameters determine the magnitude of intrusion (Chapman 1988), we used Spearman's rank correlation to determine relationships, from September through March, between increases in fine sediment content and water depth, water velocity, and F_r for each redd.

Results

We observed embryos in 64% (28 of 44) of September egg pocket samples. Kokanee significantly altered substrate during redd excavation. Analysis of substrate samples (average size 3380 g) indicated that mean percent fine sediment (< 0.83 mm) of egg pocket samples obtained in September after spawning (9.11%) was significantly (U = 180; P < 0.01) less than that in prespawn conditions (17.1%, Figure 5). Mean fine sediment content in tailspills (13.4%) was also significantly (U = 367; P = 0.01) less than in prespawn conditions (Figure 5). The difference in fine sediment content between egg pockets and tailspills was not significant (Wilcoxon T = 136; P = 0.13). Percent coarse

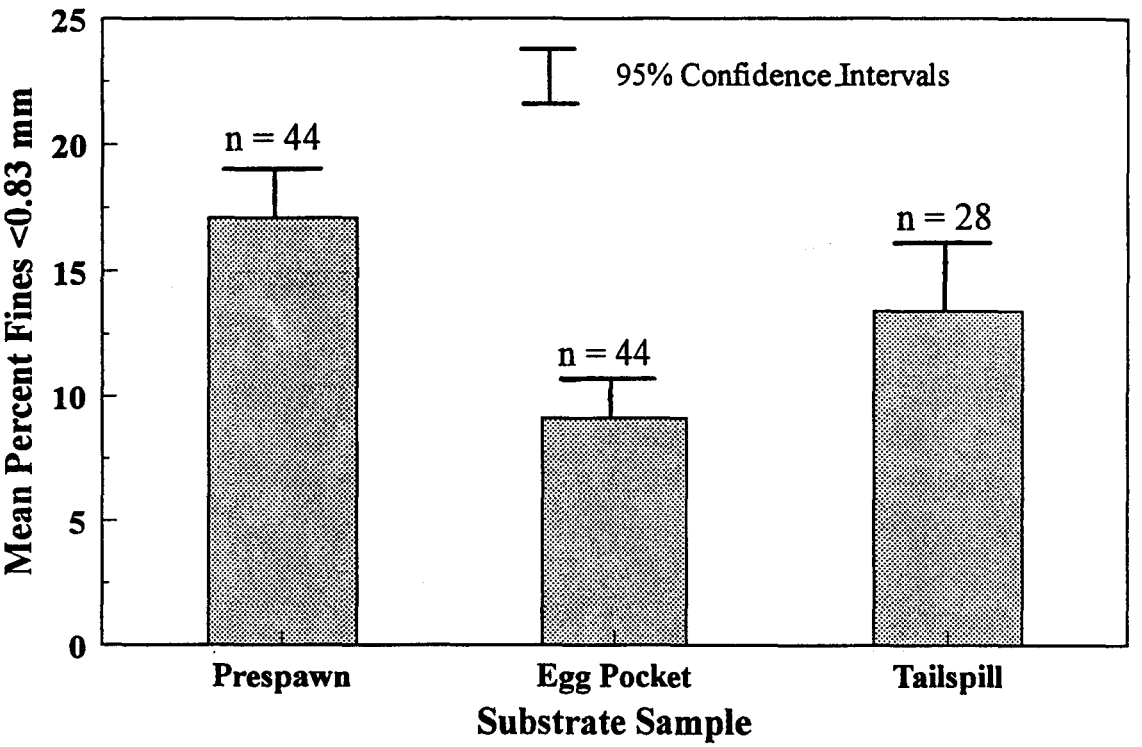

Figure 5. Comparison of estimated prespawning fine sediment (< 0.83 mm) content to samples obtained in September 1993 from estimated egg pocket and tailspill locations. Position of redds in enclosures precluded sampling of more than 28 tailspills.

gravel (19 - 76 mm) was significantly (P = 0.04) higher in egg pockets (16.0%) than in tailspills (12.7%).

In all, 19 of the 44 redds were not sampled in March due to dewatering (Site A) or altered flows from construction of a beaver dam (Site C). The Friedman test on the remaining 25 redds indicated that March fine sediments sampled in March (14.2%) were significantly (P < 0.01) higher than those sampled in September (Figure 6). Graphic comparison of mean percent fines for estimated prespawning condition and three sample dates indicate that more intrusion occurred after sampling in November (Figure 7). Rank correlation analysis revealed that fine sediment of tailspill substrate was better related to prespawn substrate ($r_s = 0.89$) than was egg pocket substrate ($r_s = 0.56$). Fine sediment content of egg pocket locations was only moderately ($r_s = 0.63$) correlated to that of tailspill locations (Figure 8). Increase in percent fines (< 0.83 mm) September through March poorly correlated with F_r ($r_s = 0.14$; P = 0.42) or water velocity ($r_s = -0.01$; P = 0.94; Figure 9). Water depth was significantly, but inversely, related to increases in fine sediment ($r_S = -0.44$; P = 0.01; Figure 10).

Discussion

We found that spawning kokanee significantly reduced the level of fine sediments (< 0.83 mm) in gravels during redd construction in the NFPR. During September sampling, we observed no bedload movement of fine sediments, and flows decreased and remained low through early March. However, fine sediment content of substrate in or near egg pockets increased significantly during the incubation period. Although sediment samples from the egg pockets probably contained few complete egg pocket centrums, we believe they provided an accurate index of changes in the incubation environment. Based on substrate samples form 44 redds, kokanee spawning activity reduced the proportion of fine sediment in gravels by nearly half (17.1% - 9.1%) of that of prespawn conditions, which is more than reported for spawning brook trout in Wyoming (Young et al. 1989).

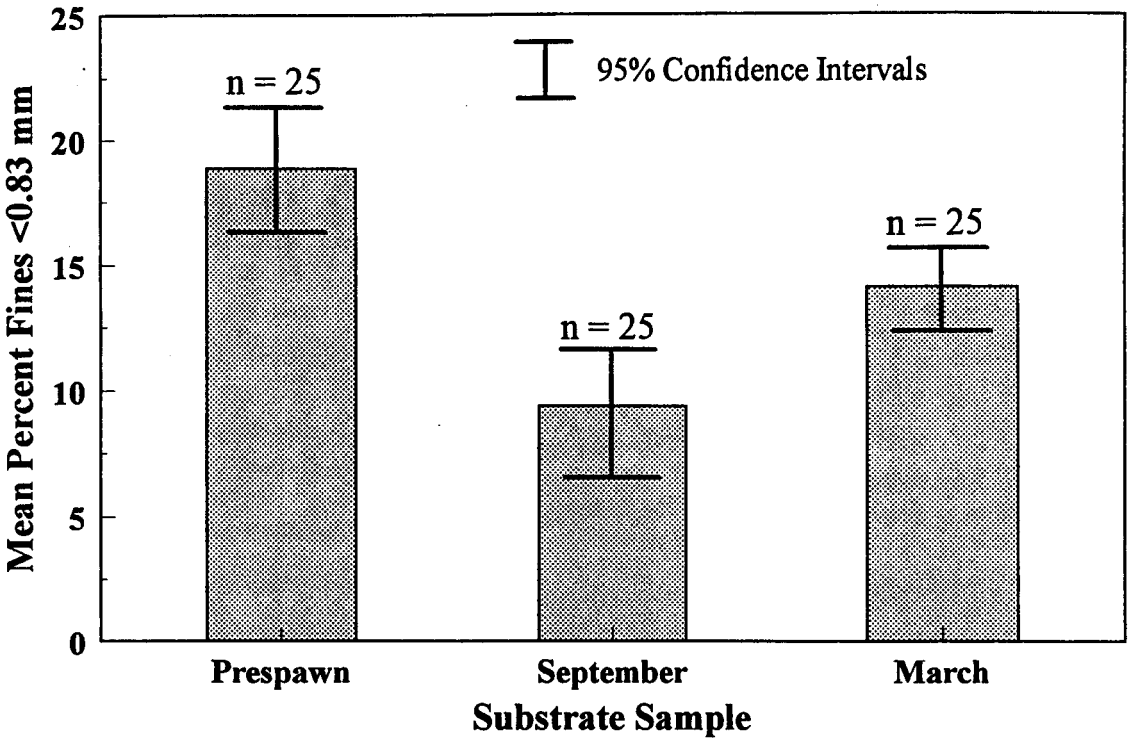

Figure 6. Comparison of prespawn estimate of fine sediments < 0.83 mm to egg pocket samples taken in September 1993 and March 1994 from 25 kokanee redds.

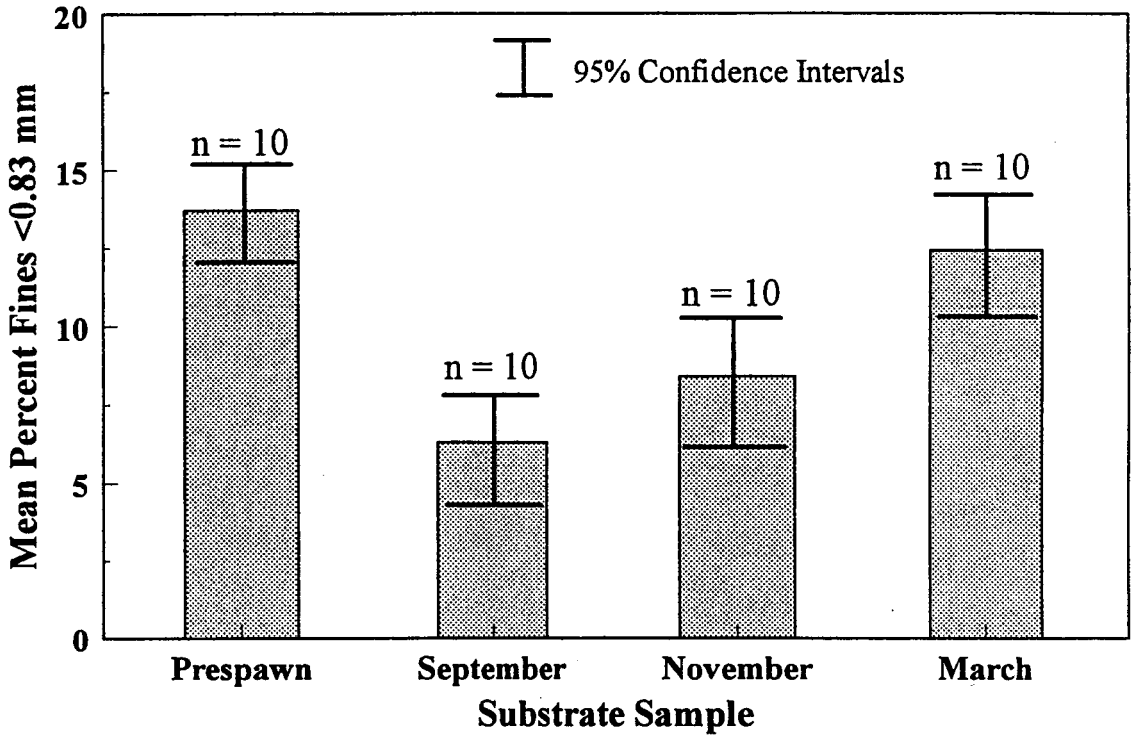

Figure 7. Mean fine sediment (< 0.83 mm) content of substrate samples obtained from egg pockets of 10 kokanee redds for three dates during incubation in 1993 to 1994. Only 10 sites were repeatedly sampled in September, November, and March because ice prevented sampling of some redds during March. Prespawn indicates estimate of mean fine sediment of substrate prior to spawning.

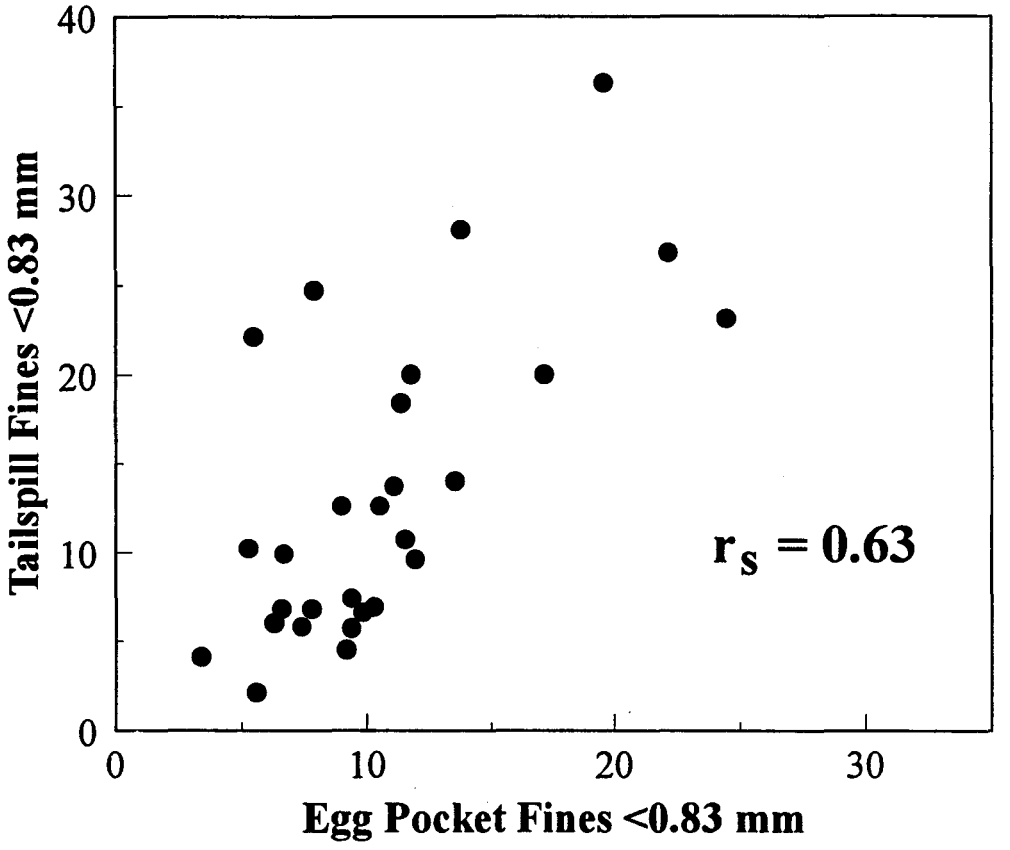

Figure 8. Comparison of fine sediment content between samples taken from egg pocket and tailspill locations in September 1993 and March 1994 from 25 kokanee redds.

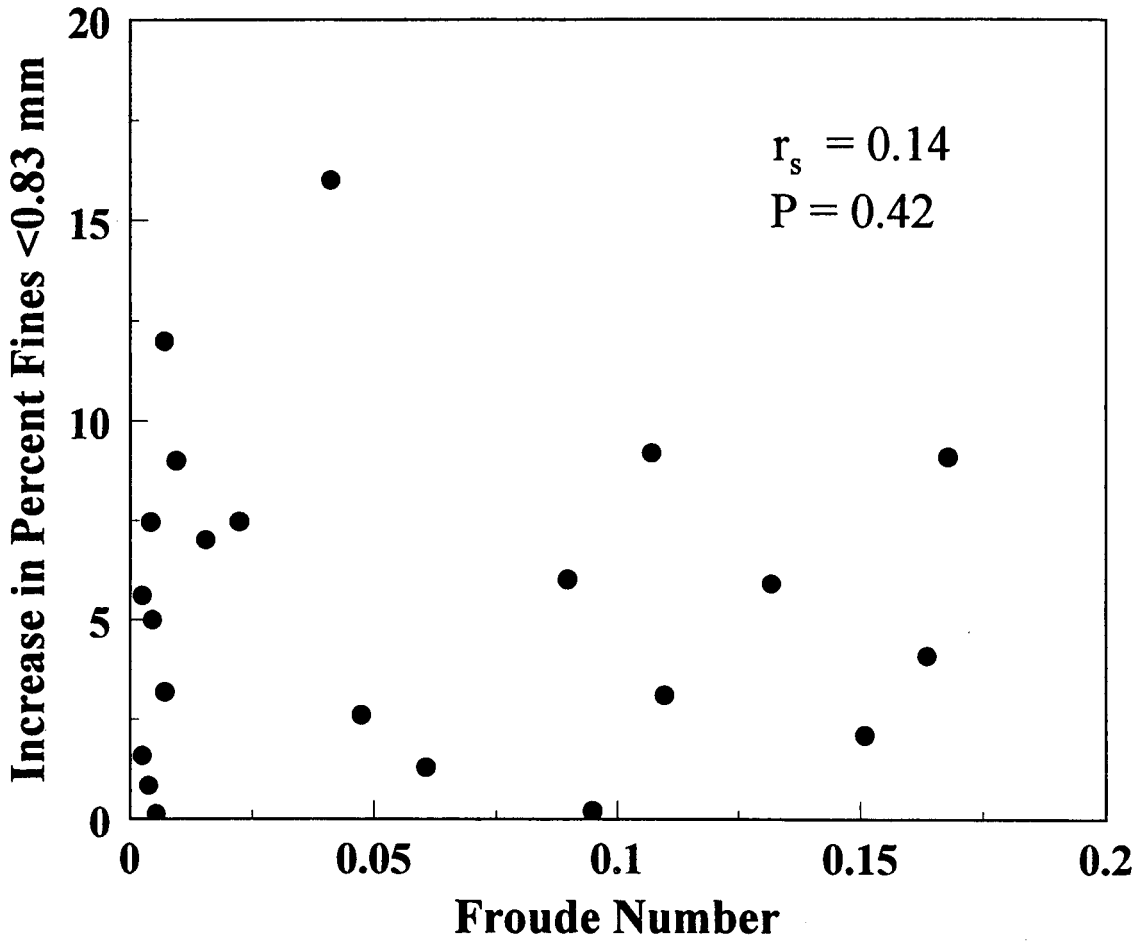

Figure 9. Relationship between increase in fine sediments (difference between September and March samples) and Froude numbers for kokanee redds sampled in 1993 to 1994.

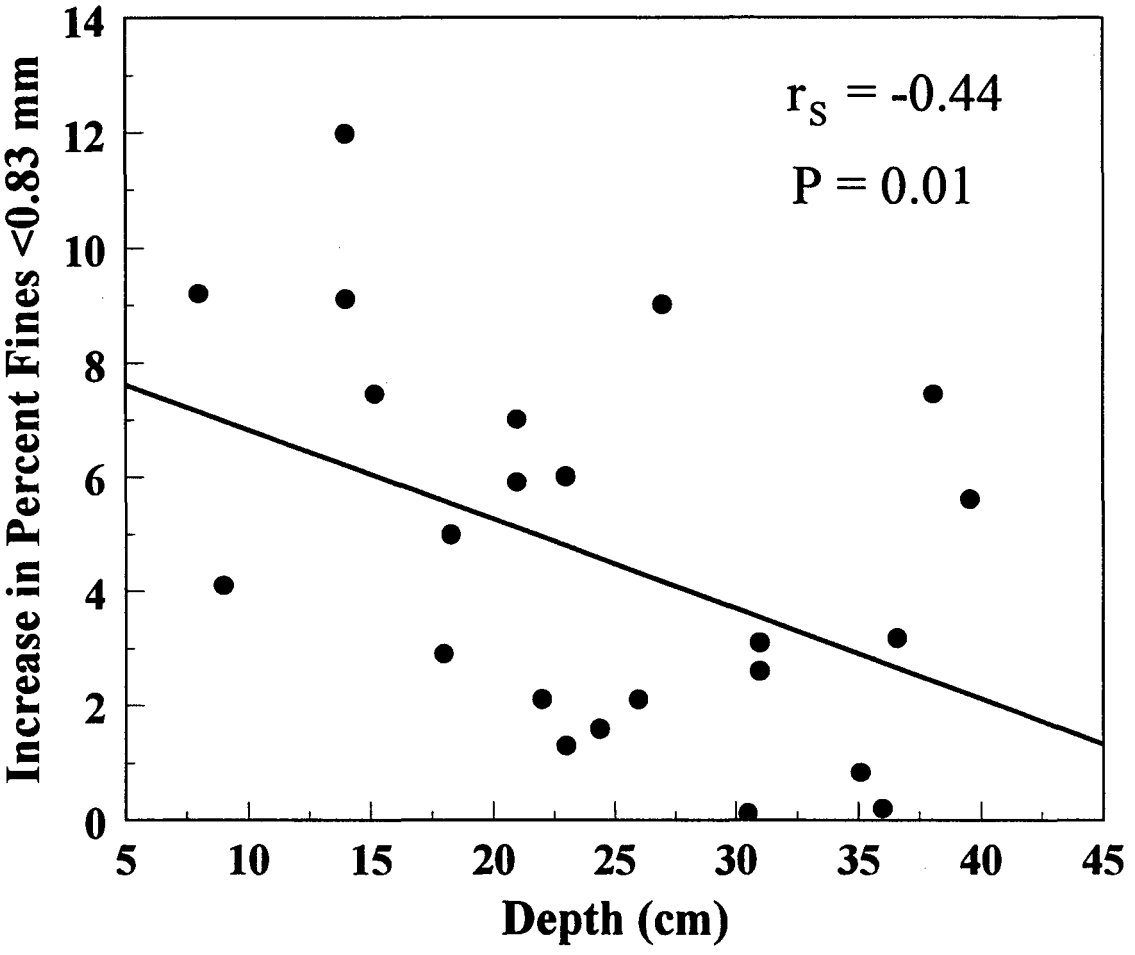

Figure 10. Relationship between increase in fine sediments < 0.83 mm and September depth measurements for kokanee redds sampled in 1993 to 1994.

Spawning kokanee in the NFPR average 340 mm in length and can probably move more material than the smaller brook trout (most < 250 mm). More importantly, kokanee spawn at high densities in the NFPR, and much of the fine sediment reduction at each redd site may be attributed to the high density of spawners. Chapman (1988) discussed how concentrated spawning by salmonids can engender a mass cleaning of fine sediments as fines removed from one redd deposit downstream, only to be lifted and passed along by females working downstream. This description accurately portrays the spawning behavior and gravel conditions in reaches of the NFPR used by spawning kokanee. Kokanee could be observed spawning at high densities bank-to-bank in several reaches more than 70 m long, and the substrate surface in some areas was a continual peak and valley contour of pits and tailspills. Our measurements of fine sediment removal by spawning kokanee, although measured for individual redds, probably reflect a cumulative effect and may over estimate effects of a single spawner. This suggests a dependent function in that, should spawner numbers decline markedly, so might the overall quality of the spawning habitat (Everest et al. 1987) and the resulting incubation success. If spawner densities decline, however, kokanee would likely spawn only in the most suitable sites that contain lower fine sediment content and are less susceptible to dewatering and freezing.

Since flows decreased to base flow by early October and remained near base flow through March sampling, we did not expect the significant increase in fines measured at egg pocket locations. Young et al. (1989) stated that streams in the central Rocky Mountains transport little sediment during fall to spring due to low or decreasing flows, which is similar to flow conditions in the NFPR. The poor correlation of increase in fine sediment content to F_r or water velocity coupled with low flows suggest that sediments intruding into kokanee redds are not being delivered by the stream.

We identified three potential sources of fine sediments intruding into kokanee redds. First, fall sampling of egg pockets may have disturbed surrounding sediments, which were deposited on other marked redds. Since redds were generally not directly

upstream or downstream of other marked redds, we do not believe this could have resulted in the dramatic increases measured in March samples. Second, later spawners may have stirred sediments that deposited on marked redds. We believe the enclosures (Objective 1) prevented later spawners from having any substantial effect. Third, and we believe more importantly, increase of fine sediments in kokanee redds during incubation may be attributed to intragravel dispersion or lateral movement of small particles. Stream-borne fine sediments are deposited in higher amounts at deeper sites with lower water velocity; however, we found a significant inverse relationship between depth and intrusion. As September flows (3.8 m^3/s) decreased to base flow in November (0.4 m^3/s) and remained low through early March, redds at shallower depths may have been covered with shallower, turbulent flow that increased intragravel movement of fine particles. Additionally, shallower sites may have experienced more substrate movement due to repeated anchor ice formation and break-up. The NFPR is typically ice-covered from November to early March. We believe these data demonstrate that fine sediments from adjacent gravels may substantially intrude into redds in the absence of freshets or flow increases usually associated with sediment transport.

Our data confirmed the finding of Young et al. (1989) that egg pocket compositions differ from other areas in the redds. In this study, we found significantly more particles 19 to 76 mm in egg pockets than in tailspills, supporting the qualitative description of redd centrum characteristics offered by Chapman (1988), that females do not move the largest particles in the substrate but rather these form the egg pocket centrum. Young et al. (1989) contended that prespawning gravel quality is a poor predictor of post-spawning gravel conditions. Although we correlated prespawning conditions with redd substrate, we do not believe this correlation is strong enough to refute their contention. Site B had substantially poorer prespawning gravel quality (27.7% < 0.83 mm) compared to sites A and B (16.0% and 13.7%, respectively). Excluding redds from site B from analysis reduced Spearman's rank correlation between prespawn and egg pocket samples

from 0.56 to 0.39. Consequently, we believe prespawning substrate condition is a poor predictor of incubation success of kokanee in the NFPR. Grost et al. (1991) contended that tailspill substrate may be representative of substrate in egg pockets later in the incubation period. Although, this study found that tailspill samples were better correlated to prespawn conditions ($r_s = 0.89$) than egg pocket conditions ($r_s = 0.63$). This may be due to large amounts of coarse granitic sand common throughout the drainage.

Our findings support the contentions of Chapman (1988) that redd centrum characteristics differ from those in other locations in the redd. Future research should focus on evaluating the importance of this difference as it relates to incubation success. We also agree with Young et al. (1989) and Lisle and Lewis (1992) that gravel samples used to predict incubation success be obtained late in the incubation period since gravel quality will likely deteriorate, especially in systems with large amounts of fine particles. For kokanee redds in this study, neither prespawning substrate quality or tailspill composition accurately represented egg pocket composition. Our data demonstrate that significant intrusion of fine sediments may occur in redds in sediment-impacted drainages, although relatively stable flows persist during incubation.

Objective 3. To evaluate the evidence of increased survival of larger kokanee embryos in a heavily sedimented stream.

Abstract

We evaluated the effect of egg size on pre-emergent survival of kokanee Oncorhynchus nerka embryos in the North Fork of the Payette River, Idaho. Results of analysis of variance indicated a positive, although marginally significant relationship between female size (estimated by embryo weight) and pre-emergent survival of kokanee.

Introduction

For more than 30 years, fisheries research in the Pacific Northwest has focused on the detrimental effects of fine sediments on salmonid embryo survival. Studies have demonstrated inverse relationships between fine sediment and embryo survival (Phillips et al. 1975; Hausle and Coble 1976; Tappel and Bjornn 1983) and between fine sediment and size of emerging fry (Shumway et al. 1963; Koski 1966; Phillips et al. 1975; Tappel and Bjornn 1983). Embryo survival has been negatively correlated with fine sediments of various sizes, ranging from less than 0.85 to 9.5 mm (Tappel and Bjornn 1983; Chapman 1988; Bjornn and Reiser 1991). Fine sediments may also entomb alevins if lateral or vertical movement of alevins is restricted by insufficient pore spaces (Phillips et al. 1975; Hausle and Coble 1976; Witzel and MacCrimmon 1981). Sediment sizes less than 0.85 mm may influence permeability of the egg pocket compared to sediments from 0.85 to 9.5 mm that primarily influence interstitial spaces (Kondolf 1988).

Other variables, including female size and egg size, may influence incubation success of salmonids. Helle (1980) reported that mean length of female chum salmon O. keta was positively correlated with survival of progeny. Larger female size may convey a social advantage to obtain the best spawning sites and attract the fittest males (Healey and Heard 1989). Larger females may also be capable of moving larger gravel (Kondolf 1988) and constructing larger redds. Van den Berghe and Gross (1984) reported strong

correlations between female size and egg depth. Crisp and Carling (1989) reported that horizontal redd dimensions (pit length, pit width, tailspill length, tailspill width) were highly correlated ($r^2 > 0.70$) to female size. Whether larger females engender increased incubation success by removing fines over a larger area or by more efficient gravel cleansing is also unknown. Female salmonids remove fine sediments from an area much wider than the egg pockets (Chapman 1988).

Egg size may also be correlated to female body size with larger eggs producing larger juveniles that have better survival (Fleming and Gross 1990). In areas of poor gravel quality, however, van den Berghe and Gross (1989) reported that egg-to-fry survival was negatively correlated with egg size. Smaller eggs may have higher rates of survival than larger eggs in systems with large concentrations of fines. The purpose of this study was to determine if egg size affected pre-emergent survival and hatching success of kokanee embryos in a heavily sedimented stream.

Methods

Newly constructed kokanee redds were located and marked from 19 through 29 September 1993 in the North Fork of the Payette River (NFPR). Individual redds were identified by their characteristic pit and tailspill and then marked by driving a numbered reinforcing bar into the substrate at the pit center. One hundred kokanee redds were identified in 11 spawning sites (Figure 2). Each site was enclosed with 3.8-cm mesh fencing to prevent further spawning to avoid superimposition of redds. Fencing was removed when most spawning activity ceased in mid-October. Each enclosure surrounded 6 to 14 kokanee redds (Table 1). Water depths and water velocities were measured at the estimated egg pocket location on the upstream one-third of the tailspill. Egg pockets of salmonids are typically found under the leading edge of the tailspill (Chapman 1988). We used a Swoffer meter to measure the water velocity at 0.6 times the water column depth; the depth where water velocity approximates mean water column velocity (Orth 1983).

Additional redds immediately adjacent to enclosures were marked and numbered similar to redds inside the enclosure. We marked redds outside each enclosure with depth, velocity, and visual substrate quality similar to redds inside enclosures.

We used a hollow core sampler (McNeil 1962) to collect substrate from 25 redds adjacent to enclosures and randomly selected redds within enclosures (Table 1). Substrate samples were collected in March at the estimated egg pocket location. These samples were dried for 4 days at 101°C and mechanically sieved for 1 minute through 12 U.S. Geological Survey standard sieves with mesh sizes from 0.25 to 76 mm. To eliminate sampling bias of underestimating larger particles, we excluded particles larger than 25 mm from analysis (Adams and Beschta 1980; Chapman et al. 1986; Young et al. 1991). We computed percent fine sediment (< 0.83 mm) from the weights of various particles. Mean percent fines (< 0.83 mm) were calculated for each enclosure. We could not core all redds because of our concern for destructive sampling, therefore we assumed estimates of gravel quality in sampled redds reflected conditions in unsampled redds.

Embryos and alevins were collected from 87 redds in enclosures by hydraulic sampling (Table 1; McNeil 1964; Magee and Heiser 1971). A portable water pump rated for 2.2 L/s was used to pump an air-water mixture through a 0.5-m^2 area of the redd believed to contain the egg pocket. The air-water mixture lifted dead and live embryos and alevins into the water column where they were collected in a 2.2-m^2 drift screen constructed of 2-mm nylon netting. Embryos and alevins were preserved in 10% buffered formalin, blotted dry, and weighed to the nearest 0.1 mg. We did not measure size of spawning females. Egg weight was used as a relative estimate of female size, as female salmonid size is correlated (r = 0.46 - 0.59) to egg weight for several species (Gall 1975; Beacham and Murray 1985; Murray et al. 1989). Fleming and Gross (1990) also found egg size correlated with body size within populations.

We estimated hatching success as the ratio of live alevins and embryos to dead embryos and alevins. We correlated egg weight and incubation success with substrate size,

water depth, and water velocity. McNeil et al. (1964) reported significant removal of dead salmonid eggs during incubation by decomposition or invertebrate predation. We found minimal (< 3%) removal of kokanee eggs during incubation in the NFPR (Objective 2), so the number of dead embryos was not adjusted for losses. Percent hatching success was not arcsine transformed since most proportions ranged from 30% to 70% (Steele and Torrie 1980). Samples collected from redds containing fewer than 25 eggs or alevins (dead or live) were excluded from analysis because we assumed these samples did not represent complete egg pockets.

Results

Percent fine sediment (< 0.83 mm) in 25 redds outside enclosures and 17 randomly selected redds inside enclosures were not significantly different ($P > 0.25$). Graphic comparison of means and range of measurements indicate that redds located outside enclosures provided valid estimates of gravel conditions of redds inside enclosures (Figure 11).

Twenty-six redds had valid estimates of egg weight and were believed representative of egg pocket sampling (> 25 embryos or alevins). Hatching success of individual redds ranged from 1% to 94%. The percentage of fines less than 0.83 mm ranged from 5% to 21% among spawning sites (Figure 11). Correlation analysis failed to reveal significant ($P > 0.05$, $r < 0.30$) relationships between individual physical habitat variables (substrate size, water depth, and velocity), egg weight, and hatching success. Results of ANOVA indicated depth, velocity, and fine sediment (< 0.83 mm) composition in March were not significantly related to incubation success ($P > 0.07$). Egg weight ($P = 0.04$) and the two-way interaction between egg weight and fine sediment content ($P = 0.04$) were significant using ANOVA type III sums of squares.

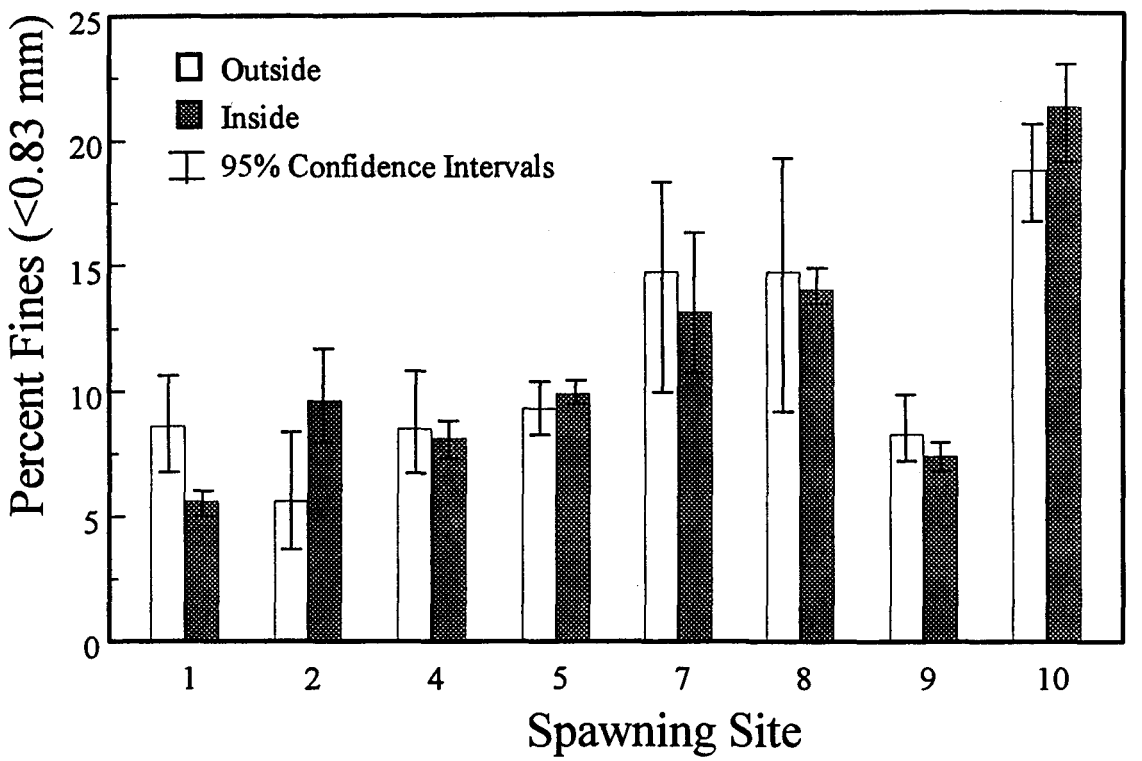

Figure 11. Comparison of mean and range of measurements of percent fine sediments < 0.83 mm in redds located inside and outside enclosures to spawning sites.

Discussion

Previous research has reported higher hatching success for smaller embryos incubated in hatcheries from smaller females for chum salmon O. keta (Beacham and Murray 1985), coho salmon O. kisutch (Allen 1957), chinook salmon O. tshawytscha (Fowler 1972), and rainbow trout O. mykiss (Murray 1980) suggesting that smaller embryos may be more viable. Van den Berghe and Gross (1989) buried coho salmon embryos of various sizes in a stream and similarly reported better survival for smaller embryos in poor-quality substrate. Results of our analysis conflict with other studies and indicate a positive relationship between egg size and incubation success of kokanee.

Egg weight was poorly correlated ($r = 0.09$) to incubation success in regression analysis (Figure 12). By controlling effects of water depth, water velocity, and substrate in the ANOVA models, we found that egg size was marginally significant in predicting pre-emergent survival of kokanee. A number of authors have reported that size of female salmonids is correlated ($r = 0.46 - 0.59$) to egg weight for several species (Gall 1975; Beacham and Murray 1985; Murray et al. 1989). Fleming and Gross (1990) also found that egg size correlated with body size within populations.

We hypothesize that larger female size has advantages associated with construction of larger redds. Increased reproductive success for larger-sized female salmonids may be influenced by larger horizontal redd dimensions or by increased efficiency in removal of fine sediments associated with a larger caudal fin and a greater finning force. We believe this hypothesis is important because, in addition to egg viability, other factors related to egg size usually result in decreased survival of larger embryos. Three possible advantages may result from construction of larger redds that could enhance incubation success. First, despite Chapman's (1988) argument that gravel conditions at the egg pocket centrum differ from surrounding redd gravels and are more important to survival than the condition of surrounding gravels, apparent water velocity through the centrum must in part depend on substrate porosity immediately upstream and downstream of the egg pocket. A broader

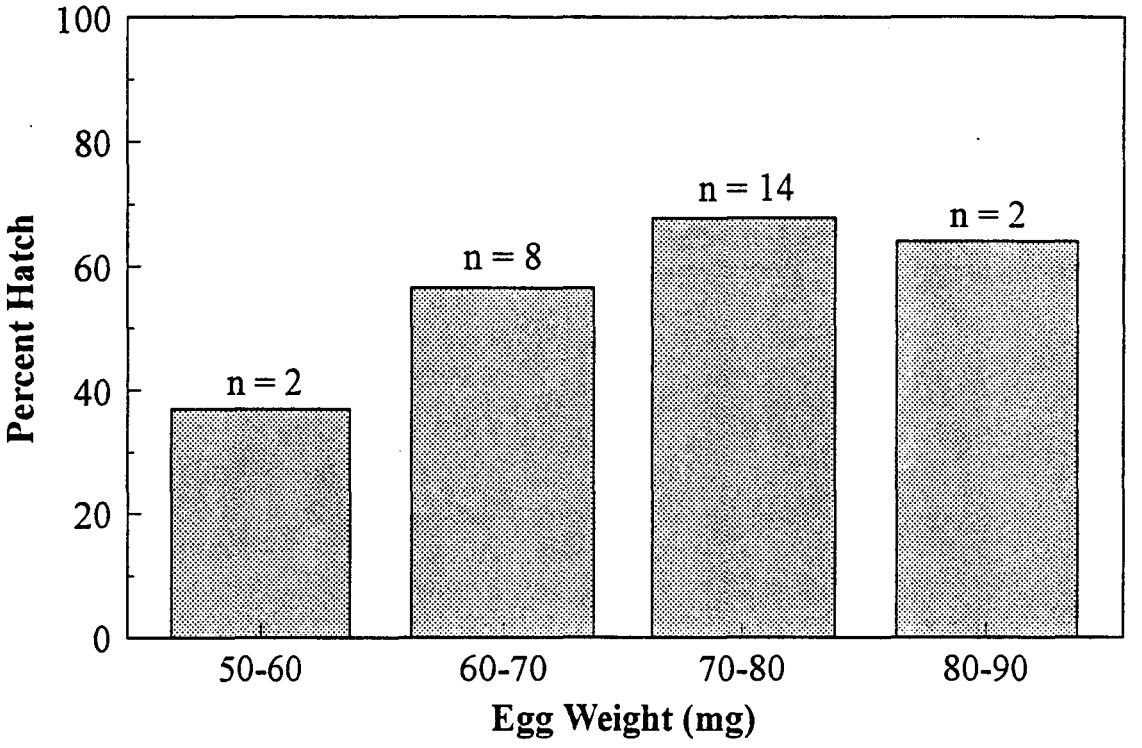

Figure 12. Relationship between percent hatch and egg weight for 26 redds in the North Fork of the Payette River in 1993 to 1994.

zone of cleaned gravels created by a larger female should enhance flow to and through the egg pocket, possibly increasing embryo survival. A wider zone of clean gravels may serve as a buffer or catchment of fine sediments when smaller particles intrude into redds during incubation, thereby preventing greater intrusion into the egg pocket. Also, larger females are more fecund and, subsequently, spawn more eggs. When oxygen delivery is marginal, redds with greater embryo densities may exhibit reduced survival and are more susceptible to fungal attack (MacKenzie and Moring 1988). Second, larger embryos have smaller surface-to-volume ratios and therefore possess less favorable gas exchange capabilities where; $S = 4\pi r^2$, $V = 4/3\pi r^3$ and $S/V = 3/r$. Third, larger embryos have a thicker boundary layer of water than smaller embryos, therefore larger embryos will have reduced oxygen uptake (Rombough 1988) than smaller embryos at the same apparent velocities.

The physical variable of fine sediment content did not significantly ($P = 0.07$) correlate with survival in this study. Although the range of fine sediment content (< 0.83 mm) measured in redds varied by a factor of three (5.0% - 14.2%), overall concentrations were low. More likely, the core samples were not stratified into redd centrum composition. Chapman (1988) stated that internal egg pocket compositions are more important to incubation success than other gravels in the redd. Core substrate samples included gravels overlying and underlying egg pockets and may have confounded the results. The marginal significance ($P = 0.04$) of the interaction between fine sediment content and egg weight does offer support for the hypothesis that more fines are removed by larger females.

Our results are limited because we did not develop a relationship between female size and egg size. We are speculating that the relationship exists for kokanee but it has never been reported. Also, it would have been beneficial to have size dimensions of the redds and relate those to female size. Our results offer evidence of a relationship not previously described and suggest new variables (egg size, female size, redd dimensions) to be included in future models predicting reproductive success of salmonids spawning in

marginal habitats.

References

Adams, J.N., and R.L. Beschta. 1980. Gravel bed composition in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 37: 1514-1521.

Alexander, D.R., and H.R. MacCrimmon. 1974. Production and movement of juvenile rainbow trout Salmo gairdneri in a headwater of Bothwell's Creek, Georgian Bay, Canada. Journal of the Fisheries Research Board of Canada 31: 117-121.

Allen, G.H. 1957. Survival through hatching of eggs from silver salmon (O. kisutch). Transactions of the American Fisheries Society 87: 207-219.

Bagliniere, J.L., G. Maisse, P.Y. Lebail, and A. Nihouarn. 1989. Population dynamics of brown trout Salmo trutta L., in a tributary on Brittany (France): Spawning and juveniles. Journal of Fish Biology 34: 97-110.

Bams, R.A. 1969. Adaptations of sockeye associated with incubation in stream gravel. Pages 71-88 *in* T.G. Northcote, editor. Salmon and trout in streams. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, Canada.

Beacham, T.D., and C.B. Murray. 1985. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (Oncorhynchus keta) from the Nitinat River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 42: 1755-1765.

Bennett, D.H., and F.O. Frost. 1995. Determination of kokanee egg-to-fry survival and spawning habitat use, the effects of land-use activities on spawning habitat and incubation success, and the potential for creating spawning habitat in the North Fork of the Payette River, Idaho. Completion Report. Project F-73-R-16. Idaho Department of Fish and Game, Boise.

Beschta, R.L., and W.L. Jackson. 1979. The intrusion of fine sediments into a stable gravel bed. Journal of the Fisheries Research Board of Canada 36: 204-210.

Bjornn, T.C., M.A. Brusven, M.P. Molhan, and J.H. Milligan. 1977. Transport of granitic sediment in streams and its effect on insects and fish. U.S. Department of Interior, Research Technical Completion Report, Project B-036-IDA.

Bjornn, T.C., and D.W. Reiser. 1991. Habitat requirements of salmonids in streams. American Fisheries Society Special Publication 19: 83-138.

Carline, R.G. 1980. Features of successful spawning site development for brook trout in Wisconsin ponds. Transactions of the American Fisheries Society 109: 453-457.

Chapman, D.W., E.E. Weitkamp, T.L. Welsh, M.B. Dell, and T.H. Schadt. 1986. Effects of river flow on the distribution of chinook salmon redds. Transactions of the American Fisheries Society 115: 537-547.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117: 1-21.

Coble, D.W. 1961. Influence of water exchange and dissolved oxygen in redds on survival of steelhead trout embryos. Transactions of the American Fisheries Society 90: 469-474.

Cordone, A.J., and D.E. Kelley. 1961. The influence of inorganic sediments on the aquatic life of streams. California Fish and Game 47: 189-228.

Crisp, D.T., T.H.K. Mann, and P.R. Cubby. 1984. Effects of impoundment upon fish populations in afferent streams at Cow Green Reservoir. Journal of Applied Ecology 21: 739-756.

Crisp, D.T., and P.A. Carling. 1989. Observations on siting, dimensions and structure of salmonid redds. Journal of Fish Biology 34: 119-134.

Crouse, M.R., C.A. Callahan, K.W. Malueg, and S.E. Dominguez. 1981. Effects of fine sediments on growth of juvenile coho salmon in laboratory streams. Transactions of the American Fisheries Society 110: 281-286.

Curry, R.A., J. Gehrels, D.L.G. Noakes, and R. Swainson. 1994. Effects of river flow fluctuations on groundwater discharge through brook trout, Salvelinus fontinalis, spawning and incubation habitats. Hydrobiologia 277: 121-134.

Daniel, W.W. 1990. Applied Nonparametric Statistics. PWS-Kent, Boston.

Erman, D.C., and G.R. Leidy. 1975. Downstream movement of rainbow trout fry in a tributary of Sagehen Creek, under permanent and intermittent flow. Transactions of the American Fisheries Society 104: 18-28.

Everest, F.H., R.L. Beschta. J.C. Scrivener, K.V. Koski, J.R. Sedell, and C.J. Cederholm. 1987. Fine sediment and salmonid production: a paradox. Pages 98-142 *in* E.O. Salo and T.W. Cundy, editors. Streamside management: forestry and fishery interactions. College of Forest Resources, University of Washington, Contribution 57, Seattle.

Everman, B.C. 1896. Salmon investigations in Idaho. Bulletin of the United States Fish Commission 15:253-289.

Fleming, I.A., and M.R. Gross. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. Ecology 71(1): 1-11.

Fowler, L.G. 1972. Growth and mortality of fingerling chinook salmon as affected by egg size. Progressive Fish-Culturist 34: 66-69.

Furniss, M.J., T.D. Roelofs, and C.S. Yee. 1991. Road construction and maintenance. American Fisheries Society Special Publication 19: 297-323.

Gall, G.A.E. 1975. Genetics of reproduction in domesticated rainbow trout. Journal of Animal Science 40: 19-27.

Gangmark, H.A., and R.D. Broad. 1955. Experimental hatching of king salmon in Mill Creek, a tributary of the Sacramento River. California Fish and Game 41: 236-241.

Gibbons, D.R., and E.O. Salo. 1973. An annotated bibliography of the effects of logging on fish of the Western United States and Canada. USDA Forest Service General Technical Report PNW-10.

Gipson, R.D., and W.A. Hubert. 1993. Spawning-site selection by kokanee along the shoreline of Flaming Gorge Reservoir, Wyoming-Utah. North American Journal of Fisheries Management 13: 475-482.

Grost, R.T., W.A. Hubert, and T.A. Wesche. 1991. Description of brown trout redds in a mountain stream. Transactions of the American Fisheries Society 120: 582-588.

Grunder, S.A., J.D. Linman, and D.R. Anderson. 1991. Federal aid in fish restoration. Regional Fishery Management Investigations, Job Performance Report, Project F-71-R-13, Idaho Department of Fish and Game, Boise.

Hansen, E.A. 1975. Some effects of groundwater on brown trout redds. Transactions of the American Fisheries Society 104: 100-110.

Harshbarger, T.J., and P.E. Porter. 1982. Embryos survival and fry emergence from two methods of planting brown trout eggs. North American Journal of Fisheries Management 2: 84-89.

Hausle, D.A., and D.W. Coble. 1976. Influence of sand in redds on survival and emergence of brook trout (Salvelinus fontinalis). Transactions of the American Fisheries Society 105: 57-63.

Haynes, J.M., and D.C. Nettles. 1983. Fall movements of brown trout in Lake Ontario and a tributary. New York Fish and Game Journal 30: 39-56.

Healey, M.C., and W.R. Heard. 1989. Inter- and intra-population variation in the fecundity of chinook salmon (Oncorhynchus tshawytscha) and its relevance to life history theory. Canadian Journal of Fisheries and Aquatic Sciences 41: 476-483.

Helle, J.G. 1980. Influence of marine environment on age and size at maturity, growth, and abundance of chum salmon Oncohynchus keta (Walbaum), from Olsen Creek, Prince William Sound, Alaska. Doctoral dissertation. Oregon State University, Corvallis.

Irving, J.S., and T.C. Bjornn. 1984. Effects of substrate size composition on survival of kokanee salmon and cutthroat and rainbow trout. Idaho Cooperative Fish and Wildlife Research Unit, Technical Report 84-6, University of Idaho, Moscow.

Kondolf, G.M. 1988. Salmonid spawning gravels: A geomorphic perspective on their size distribution, modification by spawning fish, and criteria for gravel quality. Doctoral dissertation. Johns Hopkins University, Baltimore.

Koski, K.V. 1966. The survival of coho salmon (Oncorhynchus kisutch) from egg deposition to emergence in three Oregon streams. Master's thesis. Oregon State University, Corvallis.

Koski, K.V. 1975. The survival and fitness of two stocks of chum salmon (Oncorhynchus keta) from egg deposition to emergence in a controlled stream environment at Big Beef Creek. Doctoral dissertation. University of Washington, Seattle.

Krueger, S.W. 1981. Freshwater habitat relationships, pink salmon (Oncorhynchus gorbuscha). Alaska Department of Fish and Game, Habitat Division, Anchorage.

Lisle, T.E., and J. Lewis. 1992. Effects of sediment transport on survival of salmonid embryos in a natural stream: a simulation approach. Canadian Journal of Fisheries and Aquatic Sciences 49: 2337-2344.

Lister, D.B., D.E. Marshall, and D.G. Hickey. 1980. Chum salmon survival and production at seven improved groundwater-fed spawning areas. Canadian Manuscript Report of Fisheries and Aquatic Sciences 1595.

Lorenz, J.M., and J.H. Eiler. 1989. Spawning habitat and redd characteristics of sockeye salmon in the glacial Taku River, British Columbia and Alaska. Transactions of the American Fisheries Society 118: 495-502.

MacKenzie, C., and J.R. Moring. 1988. Estimating survival of Atlantic salmon during the intragravel period. North American Journal of Fisheries Management 8: 45-49.

Magee, J.K., and D. Heiser. 1971. An improved hydraulic egg and fry sampler. Washington Department of Fisheries Report, Olympia, Washington.

Mason, J.C. 1969. Hypoxial stress prior to emergence and competition among coho salmon fry. Journal of the Fisheries Research Board of Canada 26: 63-91.

McNeil, W.J. 1962. Variations in the dissolved oxygen content of intragravel water in four spawning streams of southeastern Alaska. U.S. Fish and Wildlife Service Special Scientific Report - Fisheries 402.

McNeil, W.J. 1964. A method of measuring mortality of pink salmon eggs and larvae. United States Fish and Wildlife Service, Fisheries Bulletin 63: 575-588.

McNeil, W.J., and W.H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. U.S. Fish and Wildlife Service Special Scientific Report - Fisheries 469.

McNeil, W.J., R.A. Wells, and D.C. Brickell. 1964. Disappearance of dead pink salmon eggs and larvae from Sashin Creek, Baranof Island, Alaska. U.S. Fish and Wildlife Service, Special Scientific Report - Fisheries 485, Washington, D.C.

McNeil, W.J. 1966. Effects of the spawning bed environment on reproduction of pink and chum salmon. U.S. Fish and Wildlife Service Fishery Bulletin 65: 495-523.

Meehan, W.R., and D.N. Swanston. 1977. Effects of gravel morphology on fine sediment accumulation and survival of incubating salmon eggs. U.S. Forest Service Research Paper PNW-220.

Meehan, W.R. 1991. Introduction and overview. Pages 1-15 *in* W.R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Bethesda.

Michael, J.H. 1989. Life history of anadromous coastal cutthroat trout in Snow and Salmon creeks, Jefferson County, Washington, with implications for management. California Fish and Game 75: 188-203.

Murray, C.B. 1980. Some effects of temperature on zygote and alevin survival, rate of development and size at hatching and emergence of Pacific salmon and rainbow trout. Master's thesis. University of British Columbia, Vancouver.

Murray, C.B., J.D. McPhail, and M.L. Rosenau. 1989. Reproductive and developmental biology of kokanee from Upper Arrow Lake, British Columbia. Transactions of the American Fisheries Society 118: 5-3-509.

Neve, L.C., and V. Moore. 1983. Population estimates and size regimes of cutthroat and brook trout in Diamond, Kendall, and Spring creeks, Idaho. Northwest Science 57: 85-90.

Northcote, T.G. 1969a. Lakeward migration of young rainbow trout Salmo gairdneri in the Upper Lardeau River, British Columbia. Journal of the Fisheries Research Board of Canada 26: 33-45.

Northcote, T.G. 1969b. Patterns and mechanisms in the lakeward migratory behavior of juvenile trout. Pages 183-203 *in* T.G. Northcote, editor. Symposium of trout and salmon in streams. Vancouver, B.C., Canada.

Orth, D.J. 1983. Aquatic habitat measurements. Pages 61-84 *in* L.A. Nielsen and D.L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland

Ottaway, E.M., Carling, P.A., Clarke, A., and N.A. Reader. 1981. Observations on the structure of brown trout, Salmo trutta Linnaeus, redds. Journal of Fish Biology 19: 593-607.

Phillips, R.W., R.L. Lantz, E.W. Claire, and J.R. Moring. 1975. Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. Transactions of the American Fisheries Society 104: 461-466.

Platts, W.S., R.J. Torquemada, M.L. McHenry, and C.K. Graham. 1989. Changes in salmon spawning and rearing habitat from increased delivery of fine sediment to the South Fork of the Salmon River, Idaho. Transactions of the American Fisheries Society 118: 274-283.

Raleigh, R.T., and D.W. Chapman. 1971. Genetic control in lakeward migrations of cutthroat trout fry. Transactions of the American Fisheries Society 100: 33-40.

Reiser, D.W., and T.A. Wesche. 1977. Determination of physical and hydraulic preferences of brown and brook trout in the selection of spawning locations. Completion Report. Water Resources Research Institute, Laramie, Wyoming.

Reiser, D.W., and T.A. Wesche. 1979. In situ freezing as a cause of mortality in brown trout eggs. Progressive Fish-Culturist 41(2): 58-60.

Reiser, D.W., and R.G. White. 1981. Influence of streamflow reductions on salmonid embryo development and try quality. Idaho Water and Energy Resources Research Institute. Research Technical Completion Report, Project A-058-IDA.

Reiser, D.W., and R.G. White. 1988. Effects of two sediment size-classes on survival of steelhead and chinook salmon eggs. North American Journal of Fisheries Management 8: 432-437.

Rombough, P.J. 1988. Respiratory gas exchange, aerobic metabolism, and effects of hypoxia during early life. Pages 59-161 *in* W.S. Hoar and D.J. Randall, editors. Fish physiology, volume 11. Academic Press, San Diego, California.

Scott, W.B., and E.J. Crossman. 1973. Freshwater Fishes of Canada. Fisheries Research Board of Canada Bulletin 184.

Scrivener, J.C. 1988. Two devices to assess incubation survival and emergence of salmonid fry in an estuary streambed. North American Journal of Fisheries Management 8: 248-258.

Shapovalov, L. 1937. Experiments in hatching steelhead eggs in gravel. California Fish and Game 23: 208-214.

Shapovalov, L., and W. Berrian. 1939. An experiment in hatching silver salmon (Oncorhynchus kisutch) eggs in gravel. Transactions of the American Fisheries Society 69: 135-140.

Shaw, P.A., and J.A. Maga. 1943. The effect of mining silt on yield of fry from salmon spawning beds. California Fish and Game 29(1): 29-41.

Sheridan, W.L. 1962. Waterflow through a salmon spawning riffle in southeastern Alaska. U.S. Fish and Wildlife Service Special Scientific Report-Fisheries 407.

Shumway, D.L., C.E. Warren, and P. Doudoroff. 1963. Dissolved oxygen requirements of developing steelhead trout and chinook salmon embryos at different water velocities. Transactions of the American Fisheries Society 92: 327-343.

Snucins, E.J., R.A. Curry, and J.M. Gunn. 1992. Brook trout (Salvelinus fontinalis) embryo habitat and timing of alevin emergence in a lake and a stream. Canadian Journal of Zoology 70: 423-427.

Sowden, T.K., and G. Power. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. Transactions of the American Fisheries Society 114: 804-812.

Stauffer, T.M. 1972. Age, growth, and downstream migration of juvenile rainbow trout in a Lake Michigan tributary. Transactions of the American Fisheries Society 101: 18-28.

Steele, R.D.G., and J.H. Torrie. 1980. Principles and Procedures of Statistics. McGraw-Hill, New York.

Stowell, R., A. Espinosa, T.C. Bjornn, W.S. Platts, D.C. Burns, and J.S. Irving. 1983. Guide for predicting salmonid response to sediment yields in Idaho Batholith watersheds. U.S. Forest Service, Northern and Intermountain Regions, Ogden, Utah.

Streeter, V.L., and E.B. Wylie. 1975. Fluid mechanics. McGraw-Hill, New York.

Tappel, P.D., and T.C. Bjornn. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. North American Journal of Fisheries Management 3: 123-135.

Terhune, L.D.B. 1958. The MARK VI groundwater standpipe for measuring seepage through salmon spawning gravel. Journal of the Fisheries Research Board of Canada 15: 1027-1063.

Thurow, R.F., and J.G. King. 1994. Attributes of Yellowstone cutthroat trout redds in a tributary of the Snake River, Idaho. Transactions of the American Fisheries Society 123: 37-50.

Turnpenny, A.W.H., and R. Williams. 1980. Effects of sedimentation of the gravels of an industrial river system. Journal of Fish Biology 17: 681-693.

United States Department of Agriculture Forest Service. 1991. Environmental Impact Statement: The accelerated Engelmann spruce harvest for Brush Creek, Hendricks Creek, and Copet Creek Salvage Timber Sales. Fisheries section, pp. III/IV10-22. Payette National Forest, McCall, Idaho.

van den Berghe, E.P., and M.R. Gross. 1984. Female size and nest depth in coho salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Sciences 41: 204-206.

Wickett, W.P. 1954. The oxygen supply to salmon eggs in spawning beds. Journal of the Fisheries Research Board of Canada 11: 933-953.

Witzel, L.D., and H.R. MacCrimmon. 1981. Role of gravel substrate on ova survival and alevin emergence of rainbow trout, Salmo gairdneri. Canadian Journal of Zoology 59: 629-636.

Witzel, L.D., and H.R. MacCrimmon. 1983. Embryo survival and alevin emergence of brook char, Salvelinus fontinalis, and brown trout, Salmo trutta, relative to redd gravel composition. Canadian Journal of Zoology 61:1783-1792.

Wydowski, R.S., and D.H. Bennett. 1981. Forage species in lakes and reservoirs of the western United States. Transactions of the American Fisheries Society 110: 764-771.

Young, M.K., W.A. Hubert, and T.A. Wesche. 1989. Substrate alteration by spawning brook trout in a southeastern Wyoming stream. Transactions of the American Fisheries Society 118: 379-385.

Young, M.K., W.A. Hubert, and T.A. Wesche. 1991. Selection of measures of substrate composition to estimate survival to emergence of salmonids and to detect changes in stream substrates. North American Journal of Fisheries Management 11: 339-346.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

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